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Seasonality of Insect Succession and Pig Carcass Decomposition in a Natural Forest Area in Southeastern Brazil

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ABSTRACT: In this study, successional patterns, relative abundance of larvae and adults of sarcosaprophagous insects, carcass decay, diversity and seasonality of species, and their potential as forensic indicators were studied. Four experiments were carried out in each season in a natural area of southeastern Brazil. Two pigs (*Sus scrofa* L.) were used in each experiment and were exposed to sunlight and shade, respectively. The Calliphoridae outnumbered the Sarcophagidae in specimens collected and reared from the carcasses. More insects were collected from carcasses exposed to the sun, while a larger number of specimens were reared from those in the shade. Temperature and rainfall influenced the stages of carcass decay and insect activity and abundance. *Chrysomya albiceps* was the most abundant species in all four experiments. The carcasses were used as a protein source and substratum for oviposition. The dark putrefaction and fermentation stages yielded more flies than the other stages. These results show that flies are important in carcass decay and are, therefore, also of forensic importance. Seven species can be considered valuable forensic indicators in Southeastern Brazil. However, only three species were useful as forensic indicators in wooded areas: *P. intermutans, H. segmentaria,* and *H. semidiaphana.*

KEYWORDS: forensic science, forensic entomology, decomposition, succession, insects, carcass, Diptera, Calliphoridae, Sarcophagidae, Brazil

Decomposition of terrestrial animals, including humans, involves not only the actions of organisms such as bacteria and fungi, but also those of a large number of arthropod species, particularly the sarcosaprophagous insects (1). The rate at which decomposition progresses is further influenced by a variety of environmental factors, including temperature, humidity, precipitation, and the degree of insolation, and also by the composition of the carrion-associated fauna and the circumstances of death (2,3). Any given carcass proceeds through a process of ecological succession related to the various stages of decomposition (2,4). This succession pattern consists of the sequential addition or replacement of species within a specific community, accompanied by corresponding changes in the relative abundance of species present and localized physicochemical conditions. Such changes may result in abrupt or gradual modifications of the community (5).

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The faunal succession that occurs during decomposition is related to the natural changes that occur in the dead body. Arthropods associated with decomposition fall into four ecological categories: necrophagous species, parasites and predators of the necrophages, omnivores, and incidental or adventive species (2,6). Of these carrion fauna, several species of Calliphoridae in the genera *Lucilia, Chrysomya, Hemilucilia, Calliphora* as well as several species of Sarcophagidae are deserving of special attention (7,8). To date, most studies dealing with successional patterns in decomposition of animal remains have been conducted in temperate areas (1,4,7,8) with relatively few reports from tropical habitat (9–12). In addition to the basic ecological data, these studies provide the basis for forensic entomological investigations, since insects are among the first organisms to exploit a dead body and remain major factors throughout the entire decomposition process. Recognition of the species found during the various stages of decomposition, knowledge of the duration of each stage, combined with the influence of temperature and other environmental factors allow for the estimation of the time since death or postmortem interval in cases of death by homicide, suicide, or accident (2). The present study deals with the decomposition of animal carcasses exposed in a woodland area in southeastern Brazil. The emphasis is on the faunal diversity as indicated by the following faunistic indexes: relative abundance of adults and larvae; occurrence of each species throughout the decomposition process; relationships of the species to the carcass; differences in decomposition patterns in sunlight and shade; recognition of differences in seasonal patterns of succession; and identification of significant forensic indicator taxa.

Materials and Methods

The study was conducted in the Mata Santa Genebra Reservation located in Campinas, São Paulo State, in southeastern Brazil. This reservation, which is the largest urban reservation in South America, has a total area of approximately 250 ha and is the remnant of a primitive semidecidous mesophitic forest (13,14). The region has a rich fauna, particularly for insects and birds; however, amphibians, reptiles, and mammals are also well represented (15–16). There are seasonal variations in climatic conditions that consist of a dry cool winter occurring from early June to late August, a warm, wet summer season occurring from mid-November to late March, and two transitional seasons characterized by fluctuating temperatures and rainfall: autumn from early April to late May, and spring from early September to early November (16). The coolest month is July with a mean temperature just below 18°C, and the warmest month is January with a mean temperature above 22°C (16).

Four experiments were conducted during a one-year period, one for each season. The duration of the experiments was approximately 49 days during autumn, 45 days during winter, 35 days during spring, and 25 days during summer. During the period of this study the rainfall was recorded as follows: autumn experiment, 16.4 mm; winter, 39 mm; spring, 8.2 mm; and summer, 51.3 mm. Each experiment was continued until the entire carcass in the field was consumed and the last adult insect had emerged in the laboratory rearings. The total duration of decomposition was determined by the rate of individual carcass decay and absence or presence of insect larvae in the area. The entire process was monitored, and five stages were defined for each carcass (4). For each of the four experiments, two white domestic pigs (*Sus scrofa* Linnaeus), weighing approximately 10 kg each, were used. The pigs were taken alive to the study area and killed with a blow to the head. Care was taken to prevent external bleeding that might alter the attractiveness of the carcasses to flies or provide alternate sites for oviposition or larviposition. After death, animals were immediately placed into iron mesh cages to prevent scavenging by large vertebrates and left exposed to natural conditions. One was placed in partial sunlight in dense forest and the other in shade, separated by approximately 40 m. A tray containing sawdust was placed under each cage to facilitate the collection of larvae, leaving carcasses for pupariation. Conical traps with iron frames measuring 1.5 m diameter at the base and 1.5 m high were covered with transparent fabric and placed over the enclosure cages to collect adult insects leaving the carcasses.

Both adult and immature insects were collected on a daily basis until apparent insect activity had ceased. Collection required approximately 50 min each day, depending on the quantity of material to be collected and the weather conditions. Adult Diptera were collected using a hand net. Sawdust containing mature larvae was removed daily and taken to the laboratory in the Department of Parasitology, State University of Campinas. There, it was stored in clear, cylindrical, plastic jars measuring 15 by 25 cm until eclosion of adults.

Adult female Calliphoridae collected each day were dissected and development of their ovarioles was determined as pre-vitellogenic, vitellogenic, mature egg, and recent oviposition (17).

Faunistic indexes (FI) for three of the major families of Diptera collected (Calliphoridae, Sarcophagidae, and Muscidae) were calculated to determine the diversity of species found in the study area for each season sampled. The three faunistic indexes calculated for the collected species were the Shannon-Weiner (function H), Simpson-Yule (λ), and Hill indexes (18,19). Analysis of Variance (ANOVA) was also calculated, with the main factors being: species, stage of decomposition, insolation regimen, stage of ovarian development, and season. In all cases, response variables were the number of adults collected, day of immature collection from carcass, or day of adult emergence (considering that carcass to have been exposed on Day 1). In the later two cases, frequency was the weight variable. Interaction between species and the stage of ovarian development was also tested. Data analysis was performed using the S.A.S. (Statistical Analysis System) software (SAS, Inc. 1987). The GLM (general linear model) procedure was used for ANOVA, and the REGWF (Ryan-Einot-Gabriel-Welsch) multiple comparison F-test was used to assess the differences among the means for each factor. The TTEST procedure was used for Student t-test and the CORR procedure for correlation analysis.

Results

A total of 14 113 adult insect specimens representing 36 families (Table 1) was collected. Diptera (85%) and Coleoptera (12%) comprised 97% of the total insects collected. Among the Diptera, species in the families Calliphoridae (2971 or 20.9% of the specimens collected), Sarcophagidae (1707 or 12%), and Muscidae (3956 or 27.8%) were the most abundant. Both Diptera and Coleoptera species were recovered in every stage of decomposition. Although the conical traps used were not effective for collections of Coleoptera, a large number of species were recovered, mainly in the families Scarabaeidae (1039 or 7.3% of the total) and Histeridae (352 or 2.5%). The silphid *Oxyletrum disciolle* and the dermestid *Dermestes maculatus* were also found breeding in the carcasses.

Nine species of adult Calliphoridae were collected from carcasses during the four experiments: *Chrysomya albiceps, Chrysomya putoria, Chrysomya megacephala, Lucilia eximia, Hemilucilia segmentaria, Hemilucilia semidiaphana, Paralucilia* sp., *Cochliomyia macellaria* and *Mesembrinella bellardiana.* While most of these species were recorded throughout the year, there were some seasonal differences in relative abundance noted and different species exhibited peaks in each season. The most abundant species collected was *C. albiceps* with peaks in the autumn (185 individuals), spring (992), and summer (214). Peaks were observed in *H. seg-*

TABLE 1—*Families of insects collected in pig carcasses during four seasons from March 1994 to February 1995 at the Santa Genebra Reservation, Southeastern Brazil.*

Order	Family	Frequency
Hymenoptera	Apidae	11
	Euglossidae	4
	Formicidae	8
	Vespidae	163
Coleoptera	Dermestidae	81
	Histeridae	352
	Scarabaeidae	1.039
	Staphylinidae	82
	Silphidae	128
Hemiptera	Coreidae	2
	Reduviidae	20
Diptera	Anthomyiidae	40
	Bibionidae	11
	Bombyliidae	3
	Calliphoridae	2.971
	Dolichopodidae	4
	Drosophilidae	388
	Faniidae	997
	Lauxaniidae	5
	Micropezidae	70
	Muscidae	3.956
	Neriidae	113
	Odiniidae	22
	Otitidae	272
	Phoridae	739
	Richardiidae	1
	Ropalomeridae	3
	Sarcophagidae	1.753
	Sepsidae	425
	Syrphidae	298
	Stratiomyidae	1
	Tabanidae	94
	Tachinidae	35
	Tephritidae	20
	Tipulidae	2
Total	36 families	14.113

mentaria populations during the autumn (70 specimens) and winter (106), while a peak was noted for *L. eximia* during the winter (118 specimens). This appeared to be a successional pattern of species invasions related to stages of decomposition, but was not found to be statistically significant. At least 21 species of Sarcophagidae were collected from the carcasses: *Pattonella intermutans, Euboettcheria anguila, Euboettcheria collusor, Euboettcheria australis, Euboettcheria florencioi, Euboettcheria* sp., *Sarcodexia lambens, Oxysarcodexia* spp., *Oxysarcodexia avuncula, Oxysarcodexia thornax, Oxysarcodexia diana, Oxysarcodexia culminiforceps, Oxysarcodexia paulistanensis, Oxysarcodexia riograndensis, Adiscochaetta ingens, Squamatoides trivitattus, Chaetoravina advena, Cuculomya larvicida, Ravinia belforti, Sarcophagula* sp., *Helicobia* sp. Of these taxa, *P. intermutans* was the most significant, showing a peak in the autumn of 57 individuals collected, and was also the most abundant sarcophagid species on the carcass placed in sunlight.

A total of 75 661 flies were reared from the carcass. Of these 70 670 (93.4%) represented six species of Calliphoridae (*C. albiceps, C. putoria, L. eximia, H. segmentaria, H. semidiaphana,* and *C. megacephala*), 2081 (2.8%) of Sarcophagidae were represented by *P. intermutans,* Muscidae were represented by *Ophyra chalcogaster* with 897 individuals (1.9%) and Fanniidae with *Fannia* sp. with 2011 individuals (2.6%).

Not all species visited the carcass only to oviposit or larviposit. Some species were found visiting, copulating, and feeding on the substrate or using it as an extension of their habitat.

Insects colonizing the carcasses could be separated into four ecological categories, as noted by other workers (6). The first category, which contained the greatest number of individuals and is of highest significance in determining time since death, consisted of the necrophagous species that fed directly on the carcass. This included species in the families Calliphoridae (21% of the total), Sarcophagidae (12%), Silphidae (10%), Scarabaeidae (5.4%), and Dermestidae (0.5%), with the latter taxa being responsible for cleaning of the bones. Predators and parasites of the necrophagous species comprised the second category. Among the predators of particular significance were larvae and adults of the Coleoptera families Silphidae (10%, including necrophages), Histeridae (2.4% of the total), and Staphylinidae (0.5%), and larvae of the Diptera *C. albiceps* (7.3%), and *O. chalcogaster* (45%). While *C. albiceps* and *O. chalcogaster* fed on the carcasses, both species have been documented as also being predators during their larval stages. The third category consisted of omnivorous species (wasps, ants, and some beetles) that fed on both carcass and associated arthropods. The fourth category was comprised of incidental or adventive species having no direct relationship to the carcass. These results generally agree with those documented by Payne (8).

Discussion

Flies showed a preference for natural body openings (mouth, nose, anus) for oviposition and also hairy areas of the body with high moisture and lower intensity of light. These data are in line with observations made by Norris (20). While the Calliphoridae were more abundant during the earlier stages of decomposition, the Sarcophagidae were predominant during the later stages. Similar results were obtained by Monteiro-Filho and Penereiro (3) using rat carcasses in the same geographic area. As noted by Denno and Cothran (21), synchronous exploitation of a carcass by different families does not necessarily indicate competition, as they may use the substrate in different ways. Sarcophagids are ovoviviparous and deposit few larvae capable of immediate feeding. Therefore, larval development is rapid and they are the first ones to mature. On the other hand, calliphorid development is initially retarded due to the delay caused by the embrionation of eggs. The dominant families Calliphoridae and Sarcophagidae played a fundamental role in the carcass decomposition (Fig. 1). These families were present at carcasses in all experiments throughout the year, confirming their roles as major factors in carcass decomposition and significance to forensic entomology. As noted by Payne (8), in the absence of insects, decomposition takes significantly longer and the process remains incomplete.

As shown in Table 2, the composition and abundance of the carrion-related fauna was influenced by meteorological conditions. Season and carcass microenvironment are also factors influencing the species composition and successional patterns (22) during decomposition (Fig. 2). A low number of insects and the lowest temperature (7.5°C) were recorded during the winter (Experiment II), while the highest temperature (29.2°C) was recorded during the spring (Experiment III), when the insects were more numerous and active and the decomposition process required 35 days. The autumn study (Experiment I) appeared to be the least affected by biotic and abiotic factors, and decomposition was accomplished in 18 days. The results of the summer study (Experiment IV) were unusual in that the smallest number of adult flies were collected but the greatest number of flies were reared from the maggots collected and decomposition required only ten days.

Average rainfall during the summer was three times higher than during the other seasons. This combined with higher relative humidity during the spring and summer may have influenced the rate of decomposition. Although most species collected were present in all experiments, some distinct seasonal peaks were noted, similar to observations by Braack (23), and were replaced by other species in other seasons. While other studies have indicated no changes in carcass entomofauna due to rainfall (7,12), in this study rainfall appeared to influence adult insect activity and abundance. Heavy rains are common during the summer in southeastern Brazil, and this may have had a negative impact on adult fly abundance in the traps.

Adult Calliphoridae were collected in larger numbers from shaded carcasses but adults of other taxa were more numerous on

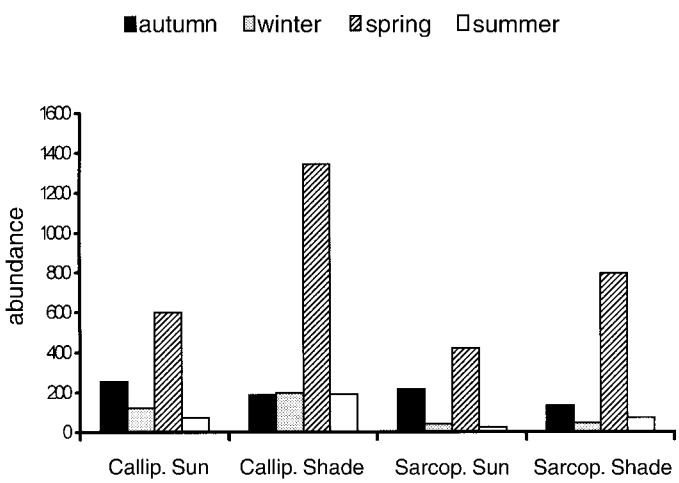

FIG. 1—*Abundance of collected adults of Calliphoridae and Sarcophagidae from pigs exposed to direct sunlight and in the shade during the four seasons at "Mata de Santa Genebra Reservation," Southeastern Brazil, from March 1994 to February 1995.*

TABLE 2—*Abundance of collected Calliphoridae and Sarcophagidae related to temperature and time of experiment and decomposition in days at the Santa Genebra Reservation, Southeastern Brazil, from March 1994 to February 1995.*

Experiment	I—Autumn	II—Winter	III—Spring	IV—Summer
Time	49	45	35	25
Decomposition	18	20	20	10
Temperature °C (min/max)	17.7/24.9	7.5/23.2	19.5/29.2	20.3/26.8
Calliphoridae				
Sun	253	120	601	75
Shade	187	196	1.344	191
Sarcophagidae				
Sun	218	39	421	26
Shade	132	45	795	73

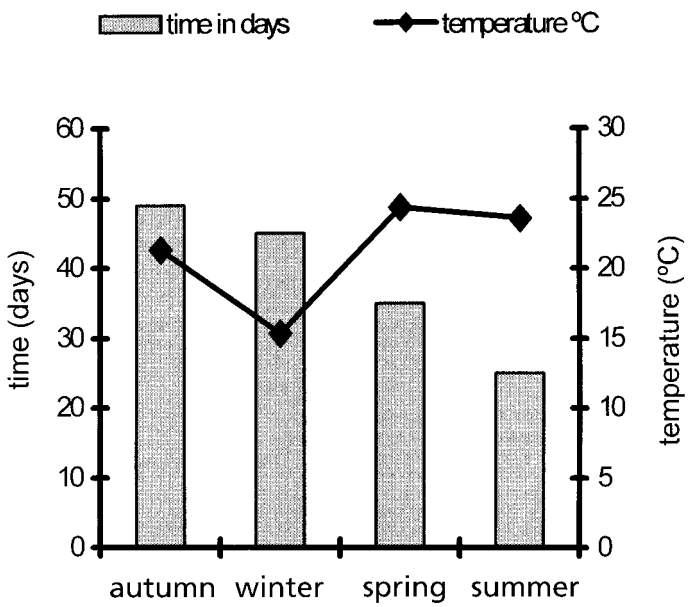

FIG. 2—*Duration of each experiment in relation to temperature during the four seasons at "Mata Santa Genebra Reservation," Southeastern Brazil, from March 1994 to February 1995.*

carcasses exposed to direct sunlight. These results are similar to those reported by Rodrigues and Bass (24) in Tennessee.

Chrysomya albiceps, C. putoria, C. megacephala, L. eximia, H. segmentaria, and *H. semidiaphana* are all good taxa for forensic use. *Hemilucilia segmentaria* and *H. semidiaphana* are also valuable indicators that the body has been in a wooded area. *Chrysomya albiceps* was the predominant species collected and reared from carcasses. This may reflect the species' high dispersal ability and arrival at carcasses shortly following death. These observations are in keeping with the fact that this exotic species has become more abundant than endemic taxa in Southeastern Brazil. While *C. albiceps* is a potential species for estimation of the postmortem interval due to its wide distribution, it is of value as an indicator of a particular habitat type, since it does not appear to display habitat specificity. While this study was conducted in a mesophytic forest habitat, *C. albiceps* was also the predominant Calliphoridae species collected from a strictly urban habitat by Souza and Linhares (12). By contrast, *H. segmentaria* and *H. semidiaphana* are present in large numbers in woodlands, but in low numbers or completely absent in urban areas. In a study conducted in both woodlands and urban situations Avancini (25) found *H. segmentaria* to be the predominant species in the woodlands and *C. megacephala* predominant in urban situations. Of the Sarcophagidae collected in this study, only *P. intermutans* was indicative of a woodland areas; once it was the only Sarcophagidae that bred in the carcasses. Laboratory studies on developmental rates of these critical species at several temperatures are now under way, and they will be of value in assessing the elapsed time of death.

Determinations of ovarian development (Table 3) showed that adult Diptera visited carcasses both to feed and/or oviposit. Female

TABLE 3—*Abundance of collected species of Calliphoridae and Sarcophagidae related to ovarian development in four experiments with pig carcasses at Santa Genebra Reservation, Southeastern Brazil, from March 1994 to February 1995.*

Species	Stages				
	Pre-Vitelogenic	Vitelogenic	Mature Egg	Oviposition	Total
Co macellaria	7	12	7	9	35
C. putoria	87	136	27	42	292
C. albiceps	175	147	68	93	483
C. megacephala	9	7	1	3	20
L. eximia	24	23	19	22	88
H. segmentaria	17	9	107	9	142
H. semidiaphana	24	17	21	9	71
Paralucilia sp	6	6	1	3	16
P. intermutans	3	8	5	3	19

Co. macellaria, C. putoria, C. albiceps, and *L. eximia* were most abundant at carcasses during their pre-vitellogenic and vitellogenic stages and were using the carcasses primarily as a source of protein. This is particularly obvious in *Co. macellaria,* which did not oviposit in the carcasses. *Hemilucilia segmentaria* was most abundant at carcasses during the mature egg stage, suggesting use of carcasses primarily for oviposition. This was the second most abundant species breeding in carcasses during this study. These observations are similar to those of Souza and Linhares (12) and Avancini (25).

Among the carrion entomofauna, Diptera larvae were the predominant primary consumers during all stages of decomposition, although the number of adults visiting carcasses decreased during the dry stage. As adult Diptera decreased, the numbers of Coleoptera increased. Coleoptera can remain active on carcasses for up to one year, depending on climatic conditions and geographic area (26).

Faunistic indexes (FI) calculated for each experiment showed a high level of diversity in the study area, since the probability of finding two individuals of the same species was low and there was a clear seasonal pattern of distribution. Thus, a relatively small number of individuals from a large number of species visited the carcasses. This is particularly true for the Sarcophagidae. Relative abundance of species within a carcass was partially defined by the species activities. Some taxa were strictly opportunistic, while other, typically more scarce taxa, became common under favorable conditions.

Conclusions

The results of this study indicate that seasonal and environmental factors are both of major significance in the process of decomposition in southeastern Brazil, influencing not only the process itself but also the composition and abundance of the carrion-entomofauna. Degree of exposure of carrion to direct sunlight has a major effect on oviposition by adult Diptera. Although a large number of insect species were observed at carcasses, relatively few used the carcass for breeding purposes. This indicates that species differ in their ability to use the various resources provided by the carcass. Generally, the first fly species to colonize the carcass had an advantage over later arriving taxa, and their larvae had a greater chance to develop to the adult stage. Both the Calliphoridae and Sarcophagidae demonstrated a preference for the dark putrefaction stage of decomposition (Stage III), although they were present in early and late stages. Exotic species of Calliphoridae, *C. albiceps,* and *C. putoria,* were observed to outnumber the endemic taxa, *H. segmentaria* and *H. semidiaphana.* While six species of Calliphoridae: *Chrysomya albiceps, C. putoria, C. megacephala, L. eximia, H. segmentaria,* and *H. semidiaphana* were useful for the determination of the postmortem interval; only *H. segmentaria* and *H. semidiaphana* were indicative of exposure in a wooded area. Of the 21 species of Sarcophagidae collected from the carcasses, only *P. intermutans* actually bred in the carcass, thus being of potential forensic significance.

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