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Distribution and abundance of forensically important flies in Santa Clara County

Adrienne Leane Brundage
San Jose State University

DISTRIBUTION AND ABUNDANCE OF FORENSICALLY IMPORTANT FLIES IN SANTA CLARA COUNTY

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Adrienne Leane Brundage

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APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

Dr. Jeffery R. Honda

Dr. Shannon Bros

Dr. Noor Tietze, Santa Clara County - Vector Control District

APPROVED FOR THE UNIVERSITY

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ABSTRACT

DISTRIBUTION AND ABUNDANCE OF FORENSICALLY IMPORTANT FLIES IN SANTA CLARA COUNTY

by Adrienne Leane Brundage

Forensic entomology has become relatively common in criminal investigations, but gaps in knowledge of local dipteran taxonomy have become apparent. These gaps led to a two-year abundance and systematics study of forensically important flies in Santa Clara County.

Four liver-baited traps were placed in each of three habitats within the county, and checked once a week for two years beginning in 2001. The result was 34,389 flies representing eight species: *Compsomyiops callipes* (Bigot 1877), *Phormia regina* (Meigen 1826), *Pollenia rudis* (Fabricus 1794), *Lucilia sericata* (Meigen 1826), *Lucilia mexicana* (Macquart 1843), *Lucilia cuprina* (Wiedemann 1826), *Calliphora vomitoria* (Linnaeus 1758), and *Calliphora latifrons* (Hough 1899). *Compsomyiops callipes* was the most abundant species in the county, while *L. mexicana* was the least abundant; *Lucilia mexicana* represents a new species record for Santa Clara County. Six species showed significant habitat preferences depending on season, while *P. regina* exhibited significant habitat preferences independent of season.

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Background

A fundamental tenet of ecology is the existence of the food web. Each species feeds on and is fed upon by organisms, facilitating the cycling of nutrients throughout the ecosystem. Each participant in the food web belongs to a trophic level based on its role in the system. Plants comprise the producer trophic level; those organisms that feed upon plants are primary consumers, and those that feed upon the primary consumers are secondary consumers (Price 1997). Nutrients cycle through the ecosystem via two major pathways: grazing and the detritus food chain (Cornaby 1974). Herbivores only consume a small portion of the above ground primary production. Decomposers or detritavores consume the balance, including the carcasses of members of the higher tropic level (Whitford 1986). Nutrients enter the decomposer subsystem via leaf, seed and fruit drop, animal defecation, and animal death. Necrophagous bacteria, fungi and animals release the nutrients from the dead tissues back into the ecosystem (Seastedt 1984). These organisms are therefore an important part of energy flow throughout the bionetwork.

Decomposer fauna are the gatekeepers to the flow of materials throughout the system, and comprise a majority of the animal species at any given terrestrial site (Hansen 2000). Large (e.g., bears, coyotes, and dogs) and small vertebrate scavengers (e.g., rodents), bacteria, fungi, and arthropods are all responsible for the cycling of nutrients back into the ecosystem (Seastedt 1984). Decomposers break down a variety of organic material, and are accordingly specialized. Each type of organic material represents an ephemeral resource that contains a variety of nutrients. The most nutrient rich resource is animal carrion, and research has shown that insects predominate as the most conspicuous, diverse and consistent group of decomposers (Catts 1992). Research into the types of insects colonizing carrion indicates three orders predominate: Coleoptera, Lepidoptera, and Diptera (Cornaby 1974). Animal carcasses can be completely skeletonized within 96 hours of death due exclusively to the voracious feeding of fly larvae. There are approximately 17,000 species of Diptera in 107 families in North America. Eighteen families represent more than one hundred species associated with decomposing carrion (Haskell 1997). The sheer number of species present makes the Diptera the most important insect order in terms of carrion reduction.

Flies inhabit two separate tropic levels: that of primary consumer as adult, and that of decomposer as larvae. Certain types of adult female Diptera are attracted to the scent of decomposing organisms, and deposit eggs on or near the food source. The eggs must be protected from direct sunlight and supplied with adequate moisture, and are therefore often laid in natural body openings. Within a few hours, depending on species and ambient temperature, the eggs hatch, and release the first of three instars of the larval stage. The first instar is tiny, often less than 2 mm in length, and may feed on the moist, mucosal areas of the eyes, nose, and mouth (Haskell 1997).

The larvae grow and molt into the second instar. This instar is the shortest of any of the life stages, often lasting no more than 8 to 12 hours. The second instar larvae feed more heavily on the body tissues due to their increased size and the natural breakdown of muscle fibers due to bacterial digestion (Hobson 1932). The second instar molts into the third instar, and continue feeding. This third stage gives rise to the huge "maggot mass" associated with advanced decomposition, and is responsible for rapid skeletonization of carrion. Maggots store the energy from the decomposing matter as fat for use as energy during the pupal stage (Haskell 1997).

After enough energy has been stored, the larvae initiate a post-feeding stage, or prepupal stage, in which the maggots cease feeding and migrate away from the food source to pupate. Larvae attempt to find a protected area in which to pupate. Pupation occurs when the outer layer of the integument hardens into a pupal casing. Within this puparium, the larvae break down and develop into the adult, winged fly. As this change progresses, the outer casing of the pupa darkens from white to brown to black, a color change that may be used to age the pupae. The adult fly emerges after several days in this state and disperses to continue the cycle (Haskell 1997).

The duration of the dipteran life cycle depends upon ambient temperature. Insects are cold-blooded organisms, and are therefore unable to regulate body temperature. Ambient temperature governs the growth rate of the larvae: the warmer the air, the faster the larvae will grow. The length of the fly's life cycle is inversely proportional to the ambient temperature. Since ambient temperature fluctuates throughout the year, flies tend to exhibit longer life cycles during the colder portions of the year (late fall through early spring) than they do during longer portions of the year (late spring through early fall) (Price 1997).

Carrion represents a temporary and ever-changing habitat and food source for a wide variety of organisms. Insects are usually the first to find such a habitat, and blowflies (Calliphoridae) in particular oviposit within hours of death. The colonization of such a habitat starts a "biological clock" and age-determination of the developing fly larvae can be used as the basis for estimating how long that carrion has been exposed to insect colonization. It is assumed that this exposure time is equal to the length of time the carrion has been dead, so larval age is directly correlated with the postmortem interval (PMI) (Catts 1992). Previous studies show that various fly species arrive in definite, predictable successional patterns, and last for a predictable amount of time, depending on temperature (Goff 1986). Given our collective knowledge of the lifecycle of the fly and the succession patterns, it is possible to figure out how long animal remains have been exposed to arthropod feeding (Smith 1986).

This ability to apply knowledge of decomposer bionomics into predicting PMI is invaluable in the field of forensics. Forensic entomology is the application of insects with respect to legal matters, and includes three major disciplines: Urban Entomology (the study of insects affecting elements of the human environment), Stored Products Entomology (the study of insects affecting food and commodities), and Medico-legal Entomology (the study of insects affecting death and decomposition). All three applications are important, but medico-legal entomology is the most common and provides biological inferences surrounding the post mortem interval (PMI) or time since death and the circumstances surrounding death. Examination of arthropods (primarily insects) collected on or near corpses provides such inferences and depends upon collection and accurate identification of species for age determination and colonization patterns (Byrd 2001).

Background and History of Forensic Entomology

The use of Forensic Entomology was first recorded in the 13th century Chinese forensic manual titled, "The Washing Away of Wrongs" (McKnight 1981). Entomology's involvement in criminal activities resurfaced in the mid-19th Century when Bergeret (1855) used insect succession to solve a case. Megnin (1894) solidified the theory of insect succession, stating that exposed remains undergo identifiable changes, and the arthropods associated with each stage appear in a regular succession. Megnin was followed by Motter (1898), who studied grave fauna. Motter discounted Megnin's theory; however, stating that the arthropods associated with interred bodies had no correlation with the length of interment. Subsequent scientists disproved Motter's conclusions, claiming a good portion of the species collected were a result of colonization before embalming (Haskell 1997).

Direct forensic entomological research is scarce in early 20th century publications. This time period was primarily focused on the taxonomy and ecology of insects of medico-criminal importance (Byrd 2001). A survey of ecological research dealing with dipteran distribution and taxonomy, carrion decomposition, and related insect species yields well over 400 papers that have forensic application (Catts 1992). More recently, forensic entomology research grew to encompass a number of topics including: the effects of certain illicit drugs on fly development, computer modeling of decay rates and successional patterns, and DNA identification of eggs, maggots and pupae (Byrd 2001).

The amount of medico-criminal entomology literature remains small when compared to other entomological fields. A recent bibliography listed 329 references directly related to forensic entomology, and three textbooks. However, scientific and law enforcement interest in the subject promises to advance the science in the years to come (Byrd 2001).

Project Scope

As forensic entomology gains acceptance, more law enforcement agencies in more areas rely upon this science in active investigations. The accuracy of entomological involvement in these investigations depends solely on the entomologist's ability to interpret the insect evidence found at the crime scene and on the body. While a great deal is known about a few species of forensically important arthropods, much more research is needed. The community of necrophagous insects differs between habitats and between geographical areas (Hanski 1976). These differences mean that general successional and life history studies may be of some use to all forensic entomologists, but accurate PMI estimation is dependent upon intimate knowledge of the immediate community makeup, specific successional patterns, and life histories of forensically important flies common in the area of the crime (Byrd 2001).

Dr. Jeff Honda at San Jose State University encountered a number of cases in the late 1990's that brought these issues to the forefront. Lack of local studies necessitated the use of general successional and life cycle data, and the use of antiquated research (J. Honda, Personal communication, September 1999). James (1955) conducted a survey of the blowflies of California by tabulating all calliphorid species curated in California entomology museums. This survey revealed 16 species found in Santa Clara County, or counties that border it (Alameda County, San Mateo County and Santa Cruz County). While this work gave insight as to which species were present in California at the time, it relied upon historical collections of fly specimens and did not focus on those of forensic importance (James 1955). Dr. Honda was able to use this limited date and successfully complete the case, but he identified two glaring gaps in the forensic entomological data specific to Santa Clara County, California: exact community makeup for this area was unknown, and prediction of individual fly species on cadavers was impossible (J. Honda, Personal communication, September 1999).

Santa Clara County, California lies at the heart of Silicon Valley, and currently supports a population of approximately 1.7 million (United States Census of Population and Housing 2001). This large population has an average mortality rate of 8681.7 persons/year. Of the 8802 deaths in 2000, 30% were investigated by the Santa Clara County's Medical Examiner's office (Santa Clara County Medical Examiner/Corner Death Statistics 2005). The Medical Examiner's office investigates deaths under suspicious circumstance and deaths occurring without a medical practitioner present. These types of death always need PMI estimation. Rigor mortis and body temperature are the most common methods of PMI estimation in recent death, but these methods are only accurate up to 72 hours after death. After

72 hours, the most accurate, although most under-utilized, method is the entomological indicators (Smith 1986).

However, using entomological indicators highlights the glaring gaps in entomological data within Santa Clara County. This lack of local insect faunal knowledge leads to a dilemma for entomologists. How can flies be used for PMI if their life cycles are unknown? Most research into forensically important flies has taken place in areas ecologically different from California: Hawaii (Early 1986, Goff 1986, 1987, 1988, 1991, 1992, 1993, 2000, 2001, 2002, 2003), Indiana (Catts 1990, 1992, Haskell 1989, 1997), West Virginia (Wells 1992, 1994, 1995, 2001), Germany (Amendt 2000, Benecke 1998, 2000, 2001, 2002, 2004), and British Columbia (Anderson 1982, 1985, 1995, 1996, 1997, 1999, 2000, 2001). While some dipterans are established worldwide, it is a well-supported fact that each microclimate supports its own unique population of insects, leading to the assumption that each microclimate supports its own unique population of decomposer flies (Hanski 1976).

The forensically important flies of Santa Clara County were surveyed to remedy this lack of local entomological data. Once the members of the local dipteran community are known, further tests to describe their life histories and improve PMI estimation can be conducted. Lt. Eric Sills of the San Jose Police Department, Homicide Unit identified the top three areas where bodies are found: on city streets or in private homes and yards (urban areas);

"floaters" in local waterways or caught along the banks of rivers or streams (riparian areas); in sparsely populated mountainous areas (rural). The objectives of the study were threefold: 1) survey the forensically important dipteran community of Santa Clara County; 2) determine if species distribution and abundance of this dipteran community significantly differ by season; 3) determine if species distribution and abundance of the dipteran community significantly differ by habitat.

Materials and Methods

A pilot study was conducted six months prior to the main study to determine the optimal type of trap, type of bait, and appropriate study sites. As a result of the pilot study, commercial wasp traps were selected and baited with 6 oz. fresh, food-grade beef liver; the liver was then covered with 8 oz of fresh water and placed in areas where decomposed bodies are typically found: Urban,[1] Riparian,[2] and Rural.[3] Trap sites matching the description of urban, riparian, and rural were identified using the 2000 US Census Report for Santa Clara County.

Urban: The urban habitat was located two miles from downtown San Jose in the surrounding suburbs. Three traps were placed in front of private homes and one near an electrical substation.

Riparian: The riparian habitat was located along Guadalupe Creek in south San Jose. One trap was placed hanging over the creek itself while the other three were placed in trees along the water's edge.

Rural: The rural area was along highways 9 and 35 in the Santa Cruz Mountains, in Saratoga. California. Four traps were placed in four turnouts along the highway near the downward slope of the mountain.

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[1] Urban: Areas that have between 500 and 1000 people per square mile (U.S. Census of Population and Housing 2001)

[2] Riparian: Areas along rivers and streams inhabited by vegetation (Klopfer 1969)

[3] Rural: Areas that have less than 500 people per square mile (U.S. Census of Population and Housing 2001)

A total of twelve traps, four in each habitat, were hung from trees at least one mile apart to discourage inter-trap competition. All traps were checked once a week from January 24, 2001 through February 28, 2003. The captured flies were preserved in 70% isopropyl alcohol and then pinned. Entomologists consider several families of flies important in forensic investigations, but consider Calliphoridae the most common and most important (Catts 1992). Current research in Indiana even indicates that Dipteran families other than Calliphoridae are superfluous to criminal investigations and should be ignored (N. Haskell, Personal communication, August 2006). Due to the overwhelming number of forensically important flies attracted by the chosen bait and traps, it was decided that only those species in the family Calliphoridae would be included in the study; all other families were preserved and stored in the J. Gordon Edwards Entomology Museum at San Jose State University for future research. Calliphorids included in the current study were identified to species (James 1955; McAlpine 1989; Whitworth 2006) and preserved in the J. Gordon Edwards Entomology Museum at San Jose State University. Identified fly species were then entered into a database for analysis.

Data were analyzed using a two-way multivariate analysis of variance (MANOVA) to determine species composition changes with habitat and/or season. A significant habitat effect indicates species composition changes depending on habitat type, while a significant interaction between habitat and season indicates that habitat changes in species composition depend upon season.

A series of two-way analysis of variance (ANOVA) were used to examine changes in abundance of specific species with respect to season and habitat. For a species, if the habitat*season interaction was not significant, and there was a significant habitat effect then two *a priori* comparisons were conducted: 1) urban vs. non-urban (riparian and rural) habitats and 2) rural vs. riparian habitats. If there was no significant habitat*season interaction and there was a significant seasonal effect, then three a priori comparisons were conducted: 1) warm (spring and summer) vs. cool (fall and winter) seasons, 2) summer vs. spring, and 3) fall vs. winter (SYSTAT 10 2002).

Results

Over two years, a total of 40,404 Calliphorid specimens were collected. However trapping methods caused damage to a number of specimens, and only 34,389 flies were successfully identified. Eight species were represented, including *Compsomyiops callipes* (Bigot 1877), *Phormia regina* (Meigen 1826), *Pollenia rudis* (Fabricus 1794), *Lucilia sericata* (Meigen 1826), *Lucilia mexicana* (Macquart 1843), *Lucilia cuprina* (Wiedemann 1826), *Calliphora vomitoria* (Linnaeus 1758), and *Calliphora latifrons* (Hough 1899). *Lucilia mexicana* represents a new species record for Santa Clara County (Table 1).

Table 1. Species list comparing species collected in current study with those identified by James (1955)

Species	Current Study	James 1955			
County:	Santa Clara	Santa Clara	Alameda	San Mateo	Santa Cruz
Calliphora grahami		X	X	X	X
Lucilia elongata				X	
Lucilia silvarum		X	X	X	
Lucilia thatuna		X	X		
Calliphora livida		X		X	X
Calliphora terraenovae			X	X	
Calliphora vicina			X	X	X
Calliphora vomitoria	X	X	X	X	X
Cochliomyia macellaria		X	X		
Calliphora latifrons	X	X	X	X	X
Compsomyiops callipes	X	X	X	X	X
Lucilia cuprina	X	X		X	
Lucilia mexicana	X				
Lucilia sericata	X	X	X		
Phormia regina	X	X	X	X	X
Pollenia rudis	X	X	X	X	X

Seven of the identified species were considered forensically important, as they have been recorded in the literature (Anderson 1997, Benecke 2001, Anderson 2001, Allaire 2005, Smith 1986, Leonardo 2006, Kneidel 1982, Kirkpatrick 2004). *Pollenia rudis* does not appear in the literature as a fly associated with post mortem interval, as immature stages are earthworm parasites while adults are attracted to garbage (Thomas 1973). Therefore it was not included in analysis.

The significant Habitat*Season interaction from the MANOVA showed that differences in species composition among habitats changed seasonally (Table 2).

Table 2. Two-way multivariate analysis of variance for examining effects of habitat (urban, rural, and riparian) and season (spring, summer, fall, and winter) on abundance of *C. callipes, L. sericata, L. mexicana, L. cuprina, C. vomitoria, C. latifrons,* and *P. regina*

	Pillai Trace	**df**	**F**	**P**
Habitat	0.533	16,612	13.907	<0.001
Season	0.433	24,921	6.654	<0.001
Habitat*Season	0.641	48,1860	4.635	<0.001

The univariate two-way ANOVAs showed that six species, *C. callipes, C. latifrons, C. vomitoria, L. sericata, L. cuprina,* and *L. mexicana* were primarily responsible for the interaction (Table 3). The disproportionate use of one habitat over another due to biotic and abiotic factors is termed "preference" in the literature (Thomas 1990). Henceforth, species found to be more abundant in particular habitats are assumed to have a preference for that habitat.

Table 3. Two-way multivariate analysis of variance for examining effects of habitat (urban, rural, and riparian) and season (spring, summer, fall, and winter) on abundance of *C. callipes, L. sericata, L. mexicana, L. cuprina, C. vomitoria, C. latifrons,* and *P. regina*

	Habitat		**Season**		**Habitat*Season**	
Species	**F**	**P**	**F**	**P**	**F**	**P**
C. callipes	27.550	**<0.001**	12.044	**<0.001**	5.257	**<0.001**
L. sericata	21.386	**<0.001**	7.396	**<0.001**	5.179	**<0.001**
L. mexicana	0.202	0.817	13.406	**<0.001**	4.378	**<0.001**
L. cuprina	14.301	**<0.001**	7.025	**<0.001**	2.916	**0.009**
C. vomitoria	32.390	**<0.001**	14.723	**<0.001**	8.164	**<0.001**
C. latifrons	5.497	**0.005**	6.523	**<0.001**	7.344	**<0.001**
P. regina	12.159	**<0.001**	7.468	**<0.001**	1.969	0.070

During winter months, *C. callipes* was more abundant in riparian areas and was rare in rural and urban areas (average number of adults collected per season <0.02) during this season. *Compsomyiops callipes* abundance rose in spring, and its habitat preference shifted from riparian areas to rural areas while urban areas continued to exhibit minimal abundance (average number adults collected <1). Summer months showed the highest numbers collected for this species; however habitat preference remained the same.

Fall months still showed this species demonstrated significant preference for rural habitats and also showed a decrease in abundance (Table 3) (Fig 1).

Table 3. Two-way multivariate analysis of variance for examining effects of habitat (urban, rural, and riparian) and season (spring, summer, fall, and winter) on abundance of *C. callipes, L. sericata, L. mexicana, L. cuprina, C. vomitoria, C. latifrons,* and *P. regina*

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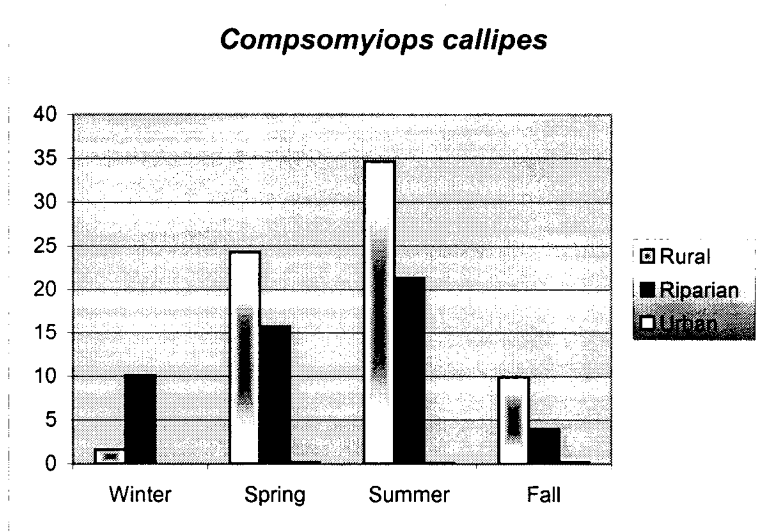

Figure 1 Average number of *Compsomyiops callipes* collected in each habitat during each season

Calliphora latifrons was the most abundant in winter, and showed the highest preference for urban habitats. Riparian habitats were favored next, while rural habitats were favored the least. In spring, overall abundance decreased, and habitat preference switched to rural habitats as the most preferred area. Urban habitats were favored next, and riparian habitats were favored least. During the summer months this species became even less abundant in all habitats, although it still preferred rural habitats. However riparian habitats were now preferred over urban habitats. *Calliphora latifrons* was least abundant in fall. However, habitat preference shifted towards urban habitats and was followed in preference by rural and riparian. Over the entire two year study, *C. latifrons* was the most abundant in urban habitats during the winter season (Table 3) (Fig 2).

Table 3. Two-way multivariate analysis of variance for examining effects of habitat (urban, rural, and riparian) and season (spring, summer, fall, and winter) on abundance of *C. callipes, L. sericata, L. mexicana, L. cuprina, C. vomitoria, C. latifrons,* and *P. regina*

	Habitat		**Season**		**Habitat*Season**	
Species	**F**	**P**	**F**	**P**	**F**	**P**
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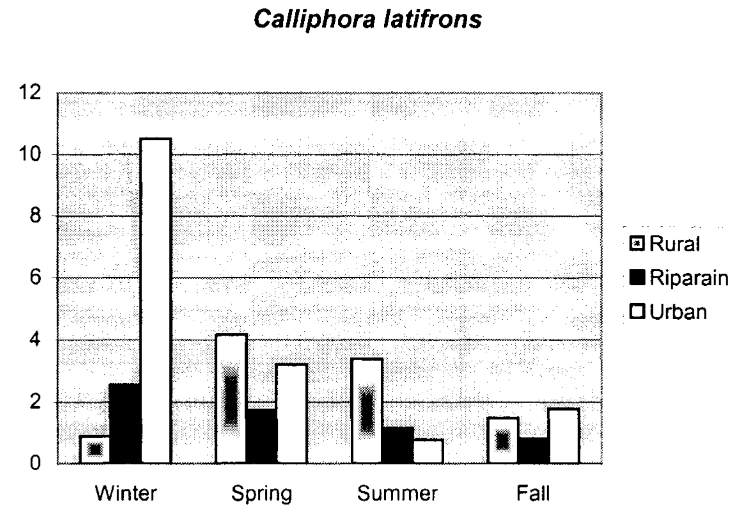

Figure 2 Average number of *Calliphora latifrons* collected in each habitat during each season

Calliphora vomitoria was least common during winter (average number <2 specimens per habitat) but was most abundant in rural areas, second most abundant in riparian areas, and least abundant in urban habitats. Spring showed a rise in abundance, and *C. vomitoria* remained most abundant in rural habitats, followed by riparian and least abundant in urban. This same habitat preference continued into the summer with a drop in overall abundance numbers. Fall months showed a dramatic decrease in abundance, mirroring those numbers observed in winter, and habitat preference remained the same. Over the entire two year study, *C. vomitoria* was significantly most abundant in rural habitats during the spring season (Table 3) (Fig 3).

Table 3. Two-way multivariate analysis of variance for examining effects of habitat (urban, rural, and riparian) and season (spring, summer, fall, and winter) on abundance of *C. callipes, L. sericata, L. mexicana, L. cuprina, C. vomitoria, C. latifrons,* and *P. regina*

Species	Habitat F	Habitat P	Season F	Season P	Habitat*Season F	Habitat*Season P
C. callipes	27.550	**<0.001**	12.044	**<0.001**	5.257	**<0.001**
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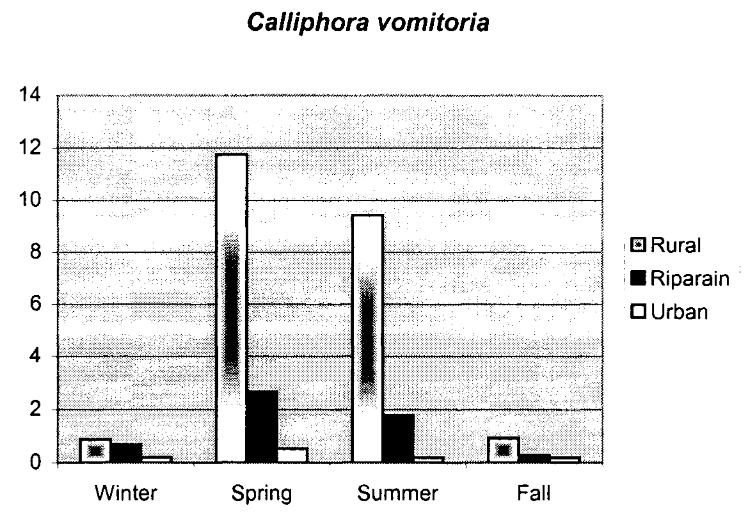

Figure 3 Average number of *Calliphora vomitoria* collected in each habitat during each season

Lucilia sericata is the first of two fly species to show more preference for urban habitats over rural and riparian. *Lucilia sericata* exhibited low abundance (average number <1) in all three habitats during the winter, but preferred rural and riparian over urban habitats. Spring showed an increase in *L. sericata* abundance, and a shift in habitat preference to urban areas. Summer months showed a slight rise in species abundance in urban areas, which continued to be the preferred habitat; however a large increase in abundance occurred in rural habitats as well. *Lucilia sericata* exhibited its greatest abundance during fall, particularly in urban areas, although abundance dropped significantly in both rural and riparian habitats. Numbers remained static throughout every season in riparian habitats, where *L. sericata* exhibited minimal abundance. Over the entire two year study, *L. sericata* was the most abundant species in urban habitats during the fall season (Table 3) (Fig 4).

Table 3. Two-way multivariate analysis of variance for examining effects of habitat (urban, rural, and riparian) and season (spring, summer, fall, and winter) on abundance of *C. callipes, L. sericata, L. mexicana, L. cuprina, C. vomitoria, C. latifrons,* and *P. regina*

	Habitat		**Season**		**Habitat*Season**	
Species	**F**	**P**	**F**	**P**	**F**	**P**
C. callipes	27.550	**<0.001**	12.044	**<0.001**	5.257	**<0.001**
L. sericata	21.386	**<0.001**	7.396	**<0.001**	5.179	**<0.001**
L. mexicana	0.202	0.817	13.406	**<0.001**	4.378	**<0.001**
L. cuprina	14.301	**<0.001**	7.025	**<0.001**	2.916	**0.009**
C. vomitoria	32.390	**<0.001**	14.723	**<0.001**	8.164	**<0.001**
C. latifrons	5.497	**0.005**	6.523	**<0.001**	7.344	**<0.001**
P. regina	12.159	**<0.001**	7.468	**<0.001**	1.969	0.070

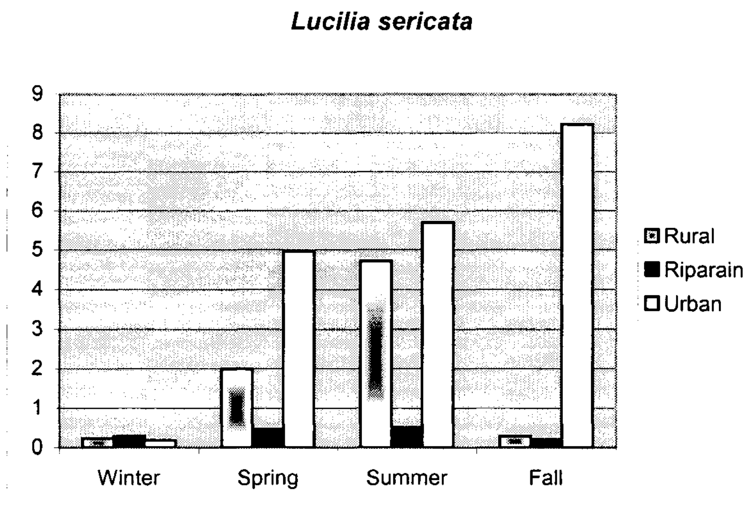

Figure 4 Average number of *Lucilia sericata* collected in each habitat during each season

Lucilia cuprina also showed preference for urban habitats and was similar to *L. sericata* in habitat preference throughout all seasons. Overall, abundance was lowest during the winter (average number <1) in all habitats, although *Lucilia cuprina* preferred riparian areas over urban areas and urban areas over rural areas. Abundance increased overall in spring, and this species showed significant preference for urban habitats over rural and riparian habitats. This pattern remained the same during the summer months, although abundance rose in urban and rural areas. Abundance decreased in fall in all habitats, but habitat preference remained the same with *L. cuprina* preferring urban habitats over riparian and rural habitats.

Over the entire two year study, *L. cuprina* was the most abundant species in urban habitats during the summer season (Table 3) (Fig 5).

Table 3. Two-way multivariate analysis of variance for examining effects of habitat (urban, rural, and riparian) and season (spring, summer, fall, and winter) on abundance of *C. callipes, L. sericata, L. mexicana, L. cuprina, C. vomitoria, C. latifrons,* and *P. regina*

	Habitat		**Season**		**Habitat*Season**	
Species	**F**	**P**	**F**	**P**	**F**	**P**
C. callipes	27.550	**<0.001**	12.044	**<0.001**	5.257	**<0.001**
L. sericata	21.386	**<0.001**	7.396	**<0.001**	5.179	**<0.001**
L. mexicana	0.202	0.817	13.406	**<0.001**	4.378	**<0.001**
L. cuprina	14.301	**<0.001**	7.025	**<0.001**	2.916	**0.009**
C. vomitoria	32.390	**<0.001**	14.723	**<0.001**	8.164	**<0.001**
C. latifrons	5.497	**0.005**	6.523	**<0.001**	7.344	**<0.001**
P. regina	12.159	**<0.001**	7.468	**<0.001**	1.969	0.070

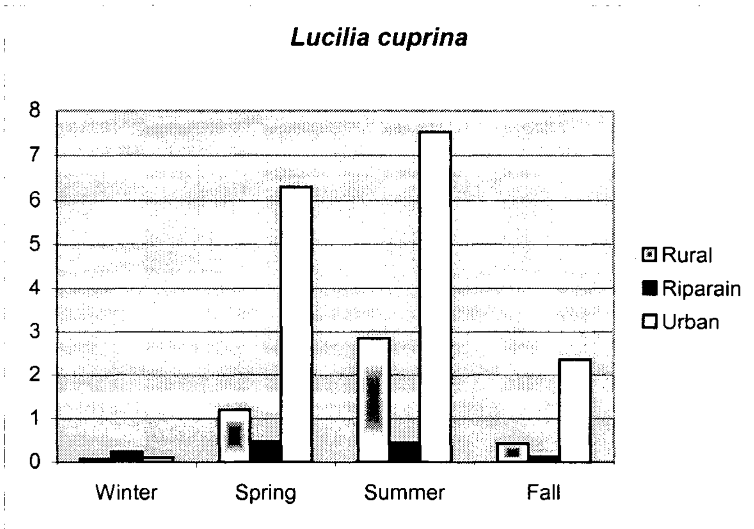

Figure 5 Average number of *Lucilia cuprina* collected in each habitat during each season

Lucilia mexicana exhibited overall low abundance (average number <2.5 flies during any season in any habitat), but exhibited definite seasonal and habitat preferences. Abundance was lowest during winter months (average number <0.5) with *L. mexicana* preferring riparian habitats to rural habitats, and rural habitats to urban habitats. Habitat preference remained constant in spring although abundance rose significantly. *Lucilia mexicana* showed most abundance overall during summer months, however showed a significant shift in habitat preferring rural habitats, followed by riparian habitats and urban habitats. Fly abundance decreased in the fall in both rural and riparian areas, but rose in urban areas. During the season, the fly preferred urban habitats over rural habitats, and showed a preference for rural habitats over riparian habitats. Over the entire two year study, *L. mexicana* was most abundant in urban habitats during the fall season (Table 3) (Fig 6).

Table 3. Two-way multivariate analysis of variance for examining effects of habitat (urban, rural, and riparian) and season (spring, summer, fall, and winter) on abundance of *C. callipes, L. sericata, L. mexicana, L. cuprina, C. vomitoria, C. latifrons,* and *P. regina*

	Habitat		**Season**		**Habitat*Season**	
Species	**F**	**P**	**F**	**P**	**F**	**P**
C. callipes	27.550	**<0.001**	12.044	**<0.001**	5.257	**<0.001**
L. sericata	21.386	**<0.001**	7.396	**<0.001**	5.179	**<0.001**
L. mexicana	0.202	0.817	13.406	**<0.001**	4.378	**<0.001**
L. cuprina	14.301	**<0.001**	7.025	**<0.001**	2.916	**0.009**
C. vomitoria	32.390	**<0.001**	14.723	**<0.001**	8.164	**<0.001**
C. latifrons	5.497	**0.005**	6.523	**<0.001**	7.344	**<0.001**
P. regina	12.159	**<0.001**	7.468	**<0.001**	1.969	0.070

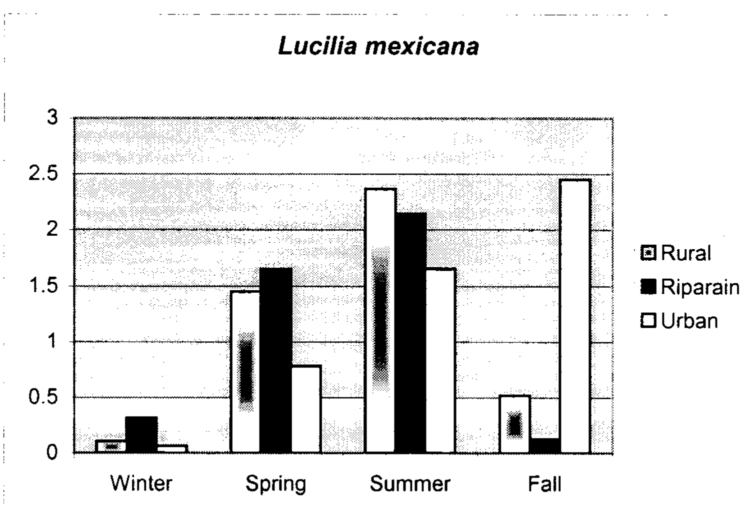

Figure 6 Average number of *Lucilia mexicana* collected in each habitat during each season

Phormia regina did not show a significant habitat*season interaction; thus habitat preference is not due to seasonal effects. A priori statistics were used to analyze seasons and locations independent of one another, and showed *Phormia regina* significantly preferred warm seasons (spring and summer) over cool seasons (fall and winter). However, it did not show any significant preference between spring and summer or fall and winter. *Phormia regina* also significantly preferred riparian and rural to urban areas with over 7000 individuals collected in these areas, versus 383 collected in urban areas over the total two year survey period. More individuals were consistently collected in riparian habitats (N=4138) than rural (N=3371), and statistical analysis showed a significant preference for riparian habitats over rural habitats (Table 4) (Fig 7).

Table 4. Two-way analysis of variance and *a priori* comparison results for examining effects of habitat (urban, rural and riparian) and season (spring, summer, fall and winter) on abundance of *P. regina*

	df	SS	MS	F	P
Season					
Warm vs. Cool	1	505.232	505.232	8.921	0.003
Spring vs. Summer	1	61.309	61.309	1.083	0.299
Fall vs. Winter	1	4.465	4.465	0.079	0.779
Habitat					
Urban vs. Non-urban	1	329.235	329.235	5.813	0.016
Riparian vs. Rural	1	1687.574	1687.574	29.797	<0.001

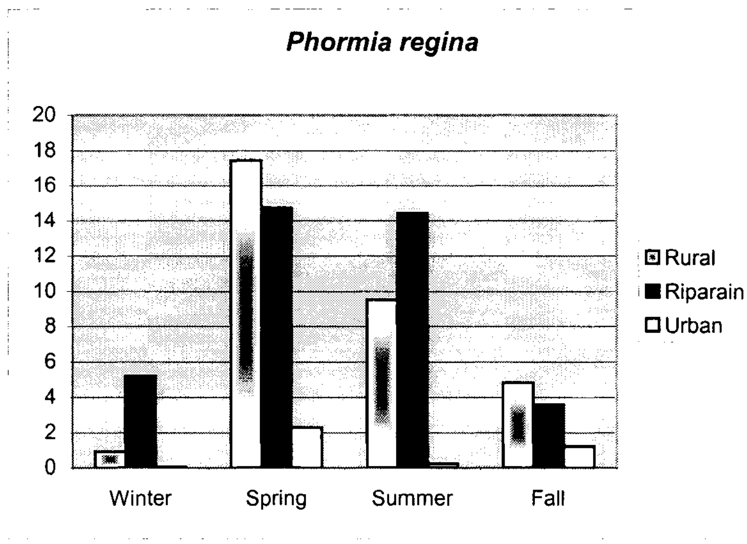

Figure 7 Average number of *Phormia regina* collected in each habitat during each season

In rural areas during winter months, investigators can assume the majority (95%) of dipteran species inhabiting a corpse will be comprised of *Compsomyiops callipes* (33.76%) *Phormia regina* (19.66%) *Calliphora vomitoria* (18.95%) *Calliphora latifrons* (18.80%) and *Lucilia sericata* (4.99%); rural carrion communities in spring will consist of *Compsomyiops callipes* (39.06%), *Phormia regina* (27.97%), *Calliphora vomitoria* (18.84%), *Calliphora latifrons* (6.69%), and *Lucilia sericata* (3.19%); while communities in summer will consist of *Compsomyiops callipes* (51.80%), *Phormia regina* (14.21%), *Calliphora vomitoria* (14.10%), *Lucilia sericata* (7.06%), *Calliphora latifrons* (5.04%), and *Lucilia cuprina* (4.25%); and fall communities will consist of *Compsomyiops callipes* (53.94%), *Phormia regina* (26.22%), *Calliphora latifrons* (8.06%), *Calliphora vomitoria* (5.08%), and *Lucilia* *mexicana* (2.83%). Riparian carrion communities mimic rural community make up with *Compsomyiops callipes* (52.71%), *Phormia regina* (27.85%), *Calliphora latifrons* (11.90%), and *Calliphora vomitoria* (2.80%) present in winter; *Compsomyiops callipes* (41.99%), *Phormia regina* (39.35%), *Calliphora vomitoria* (7.10%), *Calliphora latifrons* (4.64%), and *Lucilia mexicana* (4.40%) present in spring; *Compsomyiops callipes* (51.05%,) *Phormia regina* (34.54%), *Lucilia mexicana* (5.13%), and *Calliphora vomitoria* (4.26%) present in summer; and *Compsomyiops callipes* (43.60%), *Phormia regina* (39.47%), *Calliphora latifrons* (8.89%), and *Calliphora vomitoria* (3.07%) present in fall. Finally urban areas support markedly different carrion inhabiting communities. Thus, the majority of fly species found on a corpse in urban areas during winter months will be *Calliphora latifrons* (94.42%) and *Calliphora vomitoria* (1.81%); spring will yield *Lucilia cuprina* (34.52%), *Lucilia sericata* (27.23%), *Calliphora latifrons* (17.53%), *Phormia regina* (12.49%), and *Lucilia mexicana* (4.27%); summer months will yield *Lucilia cuprina* (46.28%), *Lucilia sericata* (35.11%), *Lucilia mexicana* (10.17%), and Calliphora latifrons (4.73%); and fall will yield *Lucilia sericata* (50.18%), *Lucilia mexicana* (14.95%), *Lucilia cuprina* (14.36%), *Calliphora latifrons* (10.84%), and *Phormia regina* (7.39%) (Table 5).

Table 5. Expected dipteran community inhabiting carrion by habitat and season, listed in order of abundance

	Winter	**Spring**	**Summer**	**Fall**
Urban	*C. latifrons* (94.42%) *C. vomitoria* (1.81%) *L. sericata* (1.59%) *L. cuprina* (0.94%) *L. mexicana* (0.58%) *P. regina* (0.51%) *C.callipes* (0.14%)	*L. cuprina* (34.52%) *L. sericata* (27.23%) *C. latifrons* (17.53%) *P. regina* (12.49%) *L. mexicana* (4.27%) *C. vomitoria* (2.90%) *C.callipes* (1.04%)	*L. cuprina* (46.28%) *L. sericata* (35.11%) *L. mexicana* (10.17%) *C. latifrons* (4.73%) *C. vomitoria* (2.01%) *P. regina* (1.30%) *C.callipes* (0.41%)	*L. sericata* (50.18%) *L. mexicana* (14.95%) *L. cuprina* (14.36%) *C. latifrons* (10.84%) *P. regina* (7.39%) *C. vomitoria* (1.17%) *C.callipes* (1.11%)
Riparian	*C. callipes* (39.06%) *P. regina* (27.97%) *C. vomitoria* (18.84%) *C. latifrons* (6.69%) *L. sericata* (3.19%) *L. mexicana* (2.33%) *L.cuprina* (1.93%)	*C. callipes* (33.76%) *P. regina* (19.66%) *C. vomitoria* (18.95%) *C. latifrons*(18.80%) *L. sericata* (4.99%) *L. mexicana*(2.28%) *L.cuprina* (1.57%)	*C. callipes* (51.80%) *P. regina* (14.21%) *C. vomitoria* (14.10%) *L. sericata* (7.06%) *C. latifrons* (5.04%) *L. cuprina* (4.25%) *L. mexicana* (3.54%)	*C. callipes* (53.94%) *P. regina* (26.22%) *C. latifrons* (8.06%) *C. vomitoria* (5.08%) *L. mexicana* (2.83%) *L. cuprina* (2.30%) *L.sericata* (1.57%)
Rural	*C. callipes* (52.71%) *P. regina* (27.85%) *C. latifrons* (11.90%) *C. vomitoria* (2.80%) *L. mexicana* (1.75%) *L. sericata* (1.64%) *L.cuprina* (1.35%)	*C. callipes* (41.99%) *P. regina* (39.35%) *C. vomitoria* (7.10%) *C. latifrons* (4.64%) *L. mexicana* (4.40%) *L. cuprina* (1.25%) *L. sericata* (1.25%)	*C. callipes* (51.05%) *P. regina* (34.54%) *L. mexicana* (5.13%) *C. vomitoria* (4.26%) *C. latifrons* (2.74%) *L. sericata* (1.22%) *L.cuprina* (1.06%)	*C. callipes* (43.60%) *P. regina* (39.47%) *C. latifrons* (8.89%) *C. vomitoria* (3.07%) *L. sericata* (2.22%) *L. mexicana* (1.38%) *L.cuprina* (1.38%)

Discussion

Different regions support different microclimates, which in turn support a unique population of carrion-breeding flies (Price 1997). Fly community and abundance is directly related to maggot infestation of carrion (Gruner 2004). The age of maggots infesting a body can be utilized by forensic entomologists to determine the post-mortem interval (Smith 1986). The current text book on forensic entomology lists those species the authors consider most important in medico-legal cases, four or which are found in Santa Clara County: *C. vomitoria, L. cuprina, L. sericata,* and *P. regina* (Byrd 2001). Their listing in such a text suggests that these are the only species that need to be studied by forensic entomologists. However, these species account for only 40% of the calliphorid species found in Santa Clara County, which clearly suggests other species have equal if not more importance in this area. Local surveys are critical in identifying what species are present in various microclimates, and therefore, what species can be expected in a medico-legal case (Tomberlin 1998).

Analysis of trap results show seven forensically important fly species present in Santa Clara County: *Compsomyiops callipes* (Bigot 1877), *Phormia regina* (Meigen 1826), *Pollenia rudis* (Fabricus 1794), *Lucilia sericata*

(Meigen 1826), *Lucilia mexicana* (Macquart 1843), *Lucilia cuprina* (Wiedemann 1826), *Calliphora vomitoria* (Linnaeus 1758), and *Calliphora latifrons* (Hough 1899) all of which show distinct seasonal and habitat preferences. These results give investigators a definite idea as to which fly species will be present in particular habitats during particular seasons within Santa Clara County. While other species will be present in small numbers, this study shows predictable numbers for any given season and habitat. If the observed community makeup on carrion is significantly different from these results, this points to an abnormality in colonization circumstances, and, depending upon the differences, may indicate movement of the decedent from one habitat to another or concealment of the decedent, thus limiting the species able to access the resource, or chemical or physical abnormalities that inhibit colonization (N. Haskell, Personal communication, 2006).

Santa Clara County's community makeup is significantly different from saprophytic dipteran communities found in other well-studied regions (Gruner 2004, Smith 1986, Byrd 2001, Goff 2000, Anderson 1996). *Compsomyiops callipes* is a species not prevalent in any other region studied and is not mentioned as forensically significant in any of the published literature, but is known to colonize human remains in areas where it is prevalent (J. Honda, Personal communication, 2004). It is found in warmer regions: Texas, Colorado, New Mexico, Arizona, Washington, California, and Mexico, and during this study was abundant year-round (James 1955). It makes up 38% of the total forensically important flies within Santa Clara County and is by far the most abundant fly here. *Phormia regina* is the second most abundant fly, although at 23% does not approach *C. callipes* in total numbers. Together, these two species make up over 60% of all flies collected in the county. The results of this survey suggest that the majority of larvae colonizing humans in Santa Clara County would most likely be *C. callipes* and *P. regina,* and is supported by forensic entomology work on numerous cases in the county (J. Honda, Unpublished data). Thus studies such as this only enforce the importance of knowing the local Diptera fauna as it allows a forensic entomologist to effectively utilize time and resources studying only those species most likely to be present, as opposed to all species known in the area.

Significant differences in species habitat preferences are clear in this study but reasons for this are unclear. Rural and riparian areas were close in species assemblage: *Compsomyiops callipes* was most abundant in both habitats with *P. regina* a close second. *Calliphora vomitoria* was third-most abundant in rural areas, but minimally abundant in riparian habitats. All other species exhibited minimal abundance in these areas. This community similarity may be due to the minimal difference between rural and riparian areas in Santa Clara County. In contrast, *C. callipes, P. regina* and *C. vomitoria* are the three least abundant flies in urban areas, which are dominated by *L. sericata, C. latifrons* and *L. cuprina. Lucilia mexicana* shows minimal abundance in all three habitats. Further studies need to be designed to more completely characterize differing habitats, and thereby quantify distinct dipteran communities.

There were also obvious seasonal variations in species assemblage; all species were found in all seasons, but in drastically different numbers. *Compsomyiops callipes* was the most abundant fly year-round, but was lowest in abundance during fall and winter. *Phormia regina* was second most abundant in winter, spring and summer, but fell to third in fall. *Calliphora latifrons* was collected predominately in summer and fall, while *C. vomitoria* was found during spring and summer. *Lucilia sericata* was found during summer and fall months, while *L. cuprina* proved to be a predominantly fall and winter fly. Finally, despite its overall low abundance, *L. mexicana* was found primarily in spring, summer and fall. All but one species showed significant habitat/season interaction, showing that habitat preference was dependent upon season. *Phormia regina* selected preferred habitats independent of season.

The effects of temperature and season on Calliphoridae are a well-studied (James 1955, Phillips 2004, Marinho 2006). Diptera inhabit a wide range of areas, and encounter a wide variety of seasonal conditions. Each species exhibits a unique set of seasonal adaptations allowing it to exploit resources in a variety of habitats. These adaptations vary greatly between species, and within species found in distinct areas, and may account for species' ability to coexist in areas with closely related and similarly adapted species (Tauber 1986). *Compsomyiops callipes* is not considered forensically or economically important in entomological literature, and therefore has not been studied in terms of seasonal distribution. This survey shows that *C. callipes* prefers the warmest months, and was most abundant during the hottest times in the county. The remaining six flies were consistent with published seasonality patterns, and exhibited no substantial deviations in Santa Clara County (Byrd 2001).

While abiotic factors account for the total range in which a particular species may be found, species interaction restricts available range and results in resource partitioning. As species diversity rises, resource competition drives niche partitioning, with each species exploiting microclimates within a habitat (Jaenike 1991). Rural and riparian areas, with their populations of large mammals probably provide a nearly endless supply of carrion. Sanitation practices in urban areas keep large carrion to a minimum, but have an abundance of alternative food sources such as garbage and compost. Insects that reside in urban areas must not only be able to withstand the environmental conditions inherent to these areas, but be able to exploit a variety of food resources effectively (Norris 1965). San Jose, CA was founded in 1777 and became characterized as an urbanized area in the early 1950s when it reached over 500 people/mi^2. Any species native to this region of California would have evolved survival strategies based upon resources present before humans urbanized the area. Total urbanization happens quickly relative to evolution, and if native flies did not already have the ability to exploit vertebrate-managed resources, then they would have been forced to retreat to areas for which they were adapted. This would have opened up urbanized areas to introduced synanthropic flies. *Lucilia* species are known to complete their life cycles on either refuse or carrion, and are therefore uniquely adapted to urban settings, while *Compsomyiops* species have only been found on carrion and were most common in this study in rural habitats (Cruickshank 2002). Research has also shown that C. *latifrons* prefers smaller carrion, and may be more adaptable to urban habitats (James 1955). These facts point to *C. callipes* being a native fly in Santa Clara County that was forced out due to urbanization and the introduction of synanthropic flies such as *L. sericata* and *L. cuprina* more suited to exploiting urban areas.

When looking at habitats individually, an interesting pattern emerges. In contrast to rural and urban areas, fly species show very little affinity for riparian habitats. *Lucilia mexicana* was the only fly to show significant preference for riparian areas. This preference was during winter and spring of each year, and then changed to rural areas during the summer and moved to urban areas in the fall. This may point to the niche exploitation by *L. mexicana*. *Lucilia mexicana* was the only fly encountered during the present survey that was not encountered in Santa Clara County, or any surrounding county, in previous studies. This species was prevalent in several counties in Southern California, as well as Sacramento and Yolo Counties in 1955 (James 1955). The past half-century appears to have seen a migration of this fly from the north and south and into the Bay Area, where it was present in limited numbers in all three habitat types during all seasons. It is the least abundant fly in the area; however, with only 1423 specimens total collected over 24 months. This may point to its recent introduction to the area. Future surveys may reveal a rise in abundance as time passes. As a relatively new fly in the area, *L. mexicana* may have trouble competing with already established species, especially if those species are closely related and therefore have similar breeding and feeding mechanisms. *Lucilia mexicana* may prefer riparian areas simply because those flies that are of greatest competition do not prefer those habitats. As *L. mexicana* abundance rises, it may be able to compete more effectively with other synanthropic flies, and therefore have no need to exploit the less desirable riparian habitats.

The diverse nature of the habitats in the Bay Area suggests a wide variety of fly species are present here. However, only seven separate species were collected and identified during this study. This differs with a species diversity study completed by James (1955) who surveyed Calliphorid collections throughout California, and reported 15 Calliphoridae species present in and around Santa Clara County. Eight of the species present in James' survey, *Calliphora grahami* (Aldrich 1930), *Lucilia thatuna* (Shannon 1926), *Lucilia elongata* (Shannon 1924), *Lucilia silvarum* (Meigen 1826), *Calliphora livida* (Hall 1948), *Calliphora terraenovae* (Macquart 1851), *Calliphora vicina* (Robineau-Desvoidy 1830) and *Cochliomyia macellaria* (Fabricus 1775) were not encountered during this project. Previous studies reveal that three of the species in James' survey are not found on carrion and therefore not considered forensically important. *Lucilia elongata, L. silvarum,* and *L. thatuna* are all known parasites of frogs and toads; *L. elongata* has been described as a facultative parasite of mammals, but no medico-legal cases featuring this species have been reported (James 1955, Dodge 1952, Bolek 2004).

The remaining five species, *C. grahami, C. livida, C. terraenovae, C. macellaria,* and *C. vicina* are all intimately associated with carrion and post mortem interval estimation, yet were not encountered during this survey (James 1955, Wang 2002, Gruner 2004, De Jong 1999, Benecke 1998, Wells

2001, Tomberline 1998). Several factors may be associated with this phenomenon: trapping methods may have been insufficient to attract these species, as they may only be attracted to large carrion, and small liver traps were used; species may not be present in sufficient numbers within the county to be encountered during a survey of this nature; local populations may have migrated away from the county or became extinct in the 52 years since James' survey due to population growth, climate change, or introduced interspecies competition; or specimens captured may have fallen into the 12.96% category left unidentifiable due to trapping methods. Further studies are needed to determine if these species are currently present in the county.

Seven of the remaining flies, *P. regina, C. latifrons, C. vomitoria, L. sericata, L. cuprina, C. callipes,* and *L. mexicana*, are all considered forensically important due to their penchant for carrion and use as indicators of post mortem interval in medico-legal cases (Goodard 1985, Gruner 2004, Anderson 1997, Benecke 2001, Anderson 2004, Smith 1981, James 1955).

Two observed phenomena within this study were not officially recorded but deserve some attention. During several weeks in the summer, one urban trap was consistently empty. This was anomalous, since calliphorids are prevalent in urban areas during the summer, and all the other traps were full. The trap was situated in an upscale neighborhood, and was undisturbed from the beginning. Inquiries at the house nearest the trap and close neighbors went unanswered. The trap was observed for several hours, and it was noticed that numerous families on the block employed a gardener. As part of his weekly chores he sprayed an unknown pesticide around each yard. It seems that the pesticide was killing off the local fly population, which is why the trap was empty. When the gardener stopped spraying for the year, the trap exhibited the same abundance of flies as the other urban traps.

The second phenomenon involved the California Bay Tree (*Umbellularia californica*), which is populous in the rural and riparian areas of the Bay Area. During the pilot study, traps hung in Bay trees attracted a much lower number of flies than those in the same area not in Bay trees. This phenomenon was especially prevalent in summer months, when the heat caused the trees to become more fragrant than they were during the cooler months. Actual trapping numbers were not analyzed to determine if the trees were having a significant effect, but the effect of bay trees on insect ability to locate resources may be an interesting area of future study.

The purpose of this study was to find out what flies of possible forensic importance are present in Santa Clara County. Now that a basic survey has been accomplished, research can begin on the most abundant species in the county: *C. callipes, P. regina, L. sericata,* and *C. latifrons* to determine the degree days, life cycle length, and rearing methods critical to medico-legal investigations. Succession studies can also be conducted to discover what order the species arrive in, and if different species are present on fresher versus older cadavers. Extensive biogeographical studies can be developed using this survey as a starting point to determine habitat delineation and possible reasons for species distribution. Habitats can be analyzed for microclimates, and a variety of niches may be identified that could help in future ecological and medico-legal cases. Finally, results of this survey can be compared to actual cases within the county to determine if the species trapped correspond to those species that actually colonize bodies.

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