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The role of community composition and basal resources in a carrion community (Diptera: Calliphoridae)

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The role of community composition and basal resources in a carrion community (Diptera:

Calliphoridae)

by

Christina LM Reid

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2012

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Calliphoridae)

by

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ABSTRACT

Mechanisms of coexistence in structured communities remain poorly understood. This study's goal was to elucidate how community composition and basal resource type mediate species interactions. A carrion community of three blow fly species, *Phormia regina* (native), *Lucilia sericata* (native), and *Chrysomya rufifacies* (invasive) (Diptera: Calliphoridae) were placed in mixed and single species communities on various food resources to examine fitness, development, and mortality changes. Food resource utilization and the interactions occurring between the species varied in each of the communities. Resource type and community composition mediated changes in *L. sericata* and *P. regina* causing shortened development times, increased mortality and decreased adult fitness when compared to single species communities. *Chrysomya rufifacies* excluded *P. regina* from some of the mixed communities. These findings suggest the potential exclusion of *P. regina* from some carrion resources and a decline in native populations and abundances in Southern Ontario, Canada if *C. rufifacies* becomes established.

DEDICATION

     I would like to dedicate this thesis to my parents Brenda and Ray for their continued support through my education and to James McLaughlin for putting in countless hours of advice, support, and research help in the work; without this my thesis would not have been completed.

ACKNOWLEDGEMENTS

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INTRODUCTION

<u>Communities</u>

According to niche theory, the ecological niche of a species subsumes all of the

interactions of the biotic and abiotic environment and represents a fundamental

ecological concept (Hutchinson 1959, Leibold 1995). A species` niche can be defined by

its life history traits, habitat, trophic position, geographic range, and other factors which

contribute to a species coexisting within its niche (Morin 1999). Fundamentally, these

additive factors can define where a species can exist, however, even when all of the

necessary factors are present and taken into account, a species may not be found in two

identical locations.

One factor to explain a species' distribution is to examine abiotic factors. A

climatic niche is the condition needed for a species to reproduce and survive (Pigot *et al*

2010). This can be conceptualized when the conditions of a climatic niche are projected

onto geographic space resulting in the distribution of a species (Colwell and Rangel

2009). Changes in elevation (Hillyer and Silman 2010), precipitation (Martin 2001),

temperature (O'Riordan *et al* 2010) and other abiotic factors can also play a crucial role

in the distribution of species.

Another explanation is to look at biotic interactions that define the realized niche

of a species. Over time, interactions between different species and among different

populations of the same species within a community determine which species are found

1

within a community at any given time (MacArthur and Levins 1967). Gause (1934) formulated the competitive exclusion principle which states that for organisms to coexist together using the same resource, each organism must have a strategy for competition against other individuals. This means that for a community to coexist over time, the different species must either use the resource in a different way or have different requirements for its realized niche.

Species within a community are a result of both biotic and abiotic factors, but a community can be defined many ways. Physically defined communities are physical locations within a habitat or particular place. Boundaries used to define these types of communities are either discrete, such as ponds, lakes, and carrion, or less discrete where the boundaries are not as clear, such as differing elevations and transitions between forests and grasslands (Morin 1999). Communities that are dominated by one or more species in abundance or biomass can be taxonomically defined. Lastly, interactively defined communities are those that one species in a particular habitat significantly influences other species abundances (Morin 1999).

A community can be comprised of many different organisms where some of the organisms acquire energy in similar ways which represents one trophic level. Interactions between different trophic levels within a community can change based on the abundances of each of the organisms, the presence or absence of organisms, or the quality or type of basal resources consumed within the community (Thebault and Loreau 2005). Interactions such as competition, predation, facilitation, and amensalism can occur either directly or indirectly between organisms within or between trophic levels. Resource partitioning has been observed in many studies across a variety of taxa (MacArthur 1958;

Huxel *et al* 2002) and explains how ecologically similar species use a resource differently and allow potential competitors to coexist (Morin 1999).

A community can be defined by the set of interactions between two or more species within a given environment. These interactions can dictate the species composition found within these communities. Competition (Hutton and Watsi 1980; Tilman 1994; Wells and Greenburg 1992) and predation (Rosa *et al* 2006) can cause shifts in the abundance of each of the different populations and subsequently cause changes in the community. As these shifts in species abundances occur, local extinctions can result (Hanski 1977).

In addition to the importance of the species composition within these communities, the resources that these species feed upon can also influence the success of different populations. When examining the second trophic level in communities, a species' fitness and development can be affected by the resources that are available for consumption (Clark *et al* 2006; Day and Wallman 2006; Ireland and Turner 2006). This could be a result of a food resource being more beneficial to one species than another and causing a change in fitness to both individuals and species. This is particularly apparent in omnivory, which is the consumption of resources at multiple trophic levels (Diehl and Feibel 2000). When omnivory, or intraguild predation as a form of omnivory, is present in a community, it can have either a stabilizing (McCann and Yodzis 1997) or destabilizing (Pimm and Lawton 1978) effect depending on the conditions of the community and the strength of the interactions between community members (Vandermeer 2006).

Omnivory, or intraguild predation, is the consumption of resources at multiple trophic levels. When omnivory is present in a community, it can have either a stabilizing (McCann and Yodzis 1997) or destabilizing (Pimm and Lawton 1978) effect depending on the conditions of the community and strength of the interactions (Vandermeer 2006). Although omnivory was once thought to be rare in nature (Holling 1959a, b), it has now been documented as a common occurrence across a variety of ecosystems. A food web that incorporates omnivory allows for the possibility of more species invasions into the chain because there are more chances for difference configurations of these webs (Law and Blackford 1992).

The introduction of an invasive species, intentional or accidental, can threaten communities that are established with all species having a specific role (Lockwood *et al* 2007). Not all invasive species become established; only species that are able to sustain their populations without more reintroductions having a chance at becoming successful (Kimberling 2004). Other factors such as sex ratios, competitive ability, dispersal rate and phenotypic plasticity can contribute to the success of an invasive species.

Carrion Insect Communities

The carrion community is a physically defined community that is ephemeral in nature and after succession of multiple insect taxa, the community disassembles when the resource is depleted (Braak 1987). Due to the volatile nature of this community, carrion based insect communities are a model system to study short term interactions between species within and between trophic levels. These communities form when a basal resource, such as an animal carcass, is presented in a variety of environments. As quickly as a few minutes after the resource is available, it can be colonized by early arriving

species. One family of insects that comprise these early colonizers is blow flies (Diptera: Calliphoridae) (Fuller 1934). The adults that arrive at the resource, oviposit their mature eggs, and leave. The offspring feed directly on the resource and complete their generation while other species continue to assemble and comprise the rest of the community. Due to the nature of the community, there are usually more individuals on the resource than can be supported. This results in a population greater than the carrying capacity (Beaver 1977; Kneidel 1984) leading to the potential for many heterospecific and conspecific interactions that may have positive, negative, or neutral effects on the current or subsequent members of the community.

Carrion communities appear to be an apparent counter-example of Gause's principle (Hanski 1981, Denno and Cothran 1975, Prinkkila and Hanski 1995); observations by Holdaway (1930) and Fuller (1934) found that there were multiple species of sarcosaprophagous species feeding on a single carrion resource. This appeared to contradict Gause's principle that two species cannot coexist indefinitely having identical niches. However, this coexistence was considered possible because each of the species would treat the carrion object not as a whole, but each specialized on different aspects of the resource (Denno and Cothran 1975, Prinkkila and Hanski 1995).

When examining the second trophic level in carrion insect communities, the sarcosaprophagous species, a species' fitness and development can be affected by the resources that are available for consumption (Clark *et al* 2006; Day and Wallman 2006; Ireland and Turner 2006). This could be a result of a food resource being more beneficial to one species than another, potentially changing the interaction outcomes between species within the community.

To evaluate which mechanisms allow apparently competing species within communities to coexist without driving each other to extinction, manipulations of the species composition and their relative abundances can be studied over a variety of basal food resource types. Lethal (mortality) and sub-lethal (fitness) effects can be examined as a measure of success of a species over a generation. Within the carrion insect community, the influence of basal carrion food resource availability and insect species composition can be easily studied due to short generation times and the ease of manipulations of the insect community composition. These carrion insect communities can consist of many difference species of blow flies (Diptera: Calliphoridae) that all feed on the decaying tissue. The addition of an omnivore that feeds both on the food resource and other species present helps to elucidate the effect the basal resource has on the community. This is due to the omnivore feeding on the basal resource and the other species feeding on the same basal resource as omnivores are more sensitive to these changes (Setala 2002). *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae) is an invasive blow fly species that becomes a facultative omnivore at the 2nd and 3rd instar stages (Shiao and Yeh 2008). It has been observed further north in the New World than ever before (Rosati and VanLaerhoven 2007) and its impact on native blow fly species has not been evaluated with respect to the regional species present here in southern Ontario. In the southern United States, *C. rufifacies* has been found in the presence of two native species, *Lucilia sericata* (Meigen) and *Phormia regina* (Meigen).

The focus of this research is to evaluate the mechanisms of coexistence that allow multiple sarcosaprophagous blow fly species (Diptera: Calliphoridae) to coexist on a single carrion food resource. To study the mechanisms of coexistence each of the study

species (*Phormia regina, Lucilia sericata,* and *Chrysomya rufifacies*) will be reared on their own on different basal carrion resources to determine if their fitness and development are influenced by what the larvae consume during development. I expect that some species will have better fitness measures, as demonstrated by a decrease in mortality and an increase in adult female size, on certain resources and this will demonstrate where they have a specialization in their niche in terms of resource requirements. The resources being used in this study are whole adult rats (representative of a whole carrion item), pig liver and cow liver (both of which are common rearing materials of blow flies) (Shiao and Yeh 2008, Day and Wallman 2006, Clark *et al* 2006) and pig skeletal muscle and cow skeletal muscle (to represent other tissues on a carrion resource). Secondly, creating communities of different compositions will evaluate what influence other larval community members have on the developmental rate, fitness and behavioural responses of individual blow fly species, and if these interactions are mediated by the basal carrion food resource type. I predict that if there is too much overlap between two blow fly species larval feeding niches', then there should be an exclusion of one of those species based on Gause's principle (Gause 1934) demonstrated by high mortality or reduced fitness of the resulting adults. However, if the species demonstrate adaptive plasticity in their feeding niche, the outcomes of the created communities should show similar ratios of adults successfully emerging regardless of some niche overlap. Lastly, evaluating if adult female size is directly correlated with fitness by measuring egg load will determine if the larval interactions are impacting the resulting adults' size and therefore fitness, with potential effects on subsequent generations. The relationship that adult size is dependent on larval nutrition was

demonstrated in *Phormia regina* (Bennettova and Fraenkel 1981) but did not determine if adult female body size and the number of ovarioles relates to female fecundity within its lifetime.

Thus, my specific objectives were to first determine if there was a relationship between adult female size and fecundity that could be used to measure fitness effects on species due to interactions occurring between species at the immature stages within different community compositions or as a result of the availability of different carrion food resource types during immature development. Secondly, I wanted to determine if facilitation, resulting greater survivorship of one species, continues between two species in the presence of a third species, an omnivore, that could be used to explain how a multispecies community can coexist over time or if it leads to the extinction of the second species with less complex interactions. Lastly, I wanted to determine if developmental plasticity results from feeding on different resources and/or if a combination of developmental plasticity and food resource partitioning is a mechanism that allows the three species of blow flies to coexist when the immatures are feeding from a single carrion resource.

METHODS

Study Species and Life Cycles

To study interactions that are occurring within the second trophic level of a carrion insect community, i.e. those insects directly consuming the resource, larvae from the blow fly family can be used. By experimentally manipulating the numbers of individuals within a community of different blow fly species and on differing basal carrion food resource types, the outcomes, strength and types of interactions occurring can be directly studied. Although all of the native blow flies are strictly sarcosaprophagous in the larval stages, several invasive blow fly species are present in North America whose larvae are facultative omnivores in the 2nd and 3rd instar stages. Using a model that contains two native blow fly species that feed only on the carrion food resource and one invasive species that feeds on both the resource and other larvae feeding on the tissue, different interactions that are naturally occurring here in Southern Ontario during the late summer and early fall months can be illuminated (Rosati and VanLaerhoven 2007) and provide insight to these interactions elsewhere. Although there are forensic case examples of single blow fly species colonizing carrion, it is far more common for multiple blow fly species to be present, all feeding on the resource at the same time. To create and study this type of community three species of blow fly (Diptera: Calliphoridae) were chosen—*Phormia regina* (Meigen)*, Lucilia sericata* (Meigen), and *Chrysomya rufifacies* (Macquart).

Phormia regina, the black blow fly from the phormiini tribe, is the dominant species during the spring, summer and fall months in Ontario (Rosati & VanLaerhoven, unpublished data) and the northern United States (Byrd and Allen 2001). It is found in temperate regions on every continent across the globe (Erzinclioglu 1988). Its role in the

carrion insect community in the second trophic level is to feed directly on the carrion resource itself, sarcosaprophagous, during its larval stages in order to acquire the nutrients to complete its development. Typically *P. regina* is considered a secondary colonizer of carrion as it arrives as a second wave of blow fly to reach a resource (Denno and Cothran 1975). This second wave however can occur within hours of the primary colonizers, and there are numerous forensic case examples of it being the sole primary colonizer of carrion (VanLaerhoven 2008). The adults of this species arrive at a resource and may feed directly on the resource by regurgitating digestive enzymes on the resource then reingesting the contents in order to acquire the protein for egg maturation or deposit their mature eggs on the resource. The eggs hatch and the larvae develop through 3 instar stages, first, second, and third as they feed on the carrion tissues by using their hook-like mouth parts to tease apart the tissues that they are feeding on (Drees and Jackman 1999). At the end of the 3rd instar stage, the larvae leave the carrion resource to pupate in the surrounding substrate and subsequently emerge as adult flies.

Lucilia sericata, the sheep blow fly, is a green bottle fly from the Luciliini tribe. It is distributed throughout the world temperate zones and can be found from Canada to Argentina in the New World (Smith 1986) and is considered to be a primary colonizer of carrion resources and is usually first to arrive to a resource (Clark *et al* 2006; Smith 1986; Denno and Cothran 1975). In Southern Ontario, *L. sericata* is most commonly present on carrion from late spring through to early fall, and frequently found together with *P. regina* (Rosati and VanLaerhoven, unpublished data). Its larval feeding and development is similar to *P. regina*.

Chrysomya rufifacies, the hairy maggot blow fly, is an invasive species, native to Australasia and the Pacific (James 1947). It was first discovered in the New World (Baumgartner and Greenberg 1984) after its initial introduction in Central America in 1978 (Jiron 1979, in Baumgartner 1993) and was recorded in the Windsor-Essex region in 2004 (Rosati and VanLaerhoven 2007). Due to its lower developmental and adult flight temperature threshold of approximately 13ºC (Vogt 2007), its distribution in North America is limited to the southern USA and Mexico during late fall, winter, spring and early summer. The longevity of the adults, 23-30 d, and their flight range, 0.84 km/d on average, allow for its easy dispersal (Tillyard and Seddon 1933; Mackerras 1933; Gurney and Woodhill 1926a). It expands its distribution up into Southern Ontario by late summer and early fall each year until temperatures force it south again (Rosati and VanLaerhoven 2007). Its success invading native communities of blow flies is due in part to its role as a secondary carrion fly (Mackerras and Fuller 1937) and its ability to switch from a sarcosaprophagous first instar larvae to a facultative predator as a second and third instar larvae feeding on hetero and conspecific larvae as well as continuing to feed on the carrion resource (James 1947; Shiao and Yeh 2008; Rosa *et al* 2006). Because *C. rufifacies* is an omnivore, the food resource type that is provided should influence its diet choice. If a more desirable resource is available, *C. rufifacies* should choose to feed more on the basal and less on the other species present in the community. Subsequently if a less desirable basal resource is provided, it should prey upon the other species causing a decrease in the survival of the other species present (Rosa *et al* 2006; Agrawal and Klein 2000).

Laboratory adult colony rearing

Adults of *Lucilia sericata* (Meigen) (Diptera: Calliphoridae) and *Phormia regina* (Meigen) (Diptera: Calliphoridae) were collected from the Windsor-Essex area in Ontario, Canada from wild fly populations. The adults were captured using King Wasp traps (www.kinghg.on.ca) baited with pig liver. Traps were placed in both sunny and shaded locations and left for 24 h. Traps were collected and flies were removed from the traps and identified to species. Adults of *L. sericata* and *P. regina* were released into separate cages (46 cm^3) containing granulated sugar cubes, water in an Erlenmeyer flask with 7 dental wicks, and skin milk powder. These provided a carbohydrate, protein, and water source for adult longevity and were replenished as needed. Pupae of *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae) were obtained from College Station, Texas collected from the field. These pupae were released into an identical cage set up as the other two species. Cages were exposed to 16:8 h light: dark cycles (Nabity *et al* 2007)

Second generation flies of each species were obtained from the established colonies by providing an oviposition medium of liver, approximately 35g, for the adult females to lay on for a 24 h period. Eggs that were laid on the medium were removed and placed on a damp paper towel, 12 cm^2, beside a 25 g piece of pig liver. The eggs, paper towel, and liver were placed in a 950 mL mason jar containing 5 cm ± 0.5 cm of beta wood chips for a pupation material (NEPCO Beta Chip). The jars were covered in black landscape material (Weed Barrier WPB 4006) with the mason ring to allow for airflow but to prevent larvae from escaping the jars. Liver was added to the jar as needed until the larvae left the food to pupate. When the adults emerged, they were released into cages identical to the first generation flies. In addition to the skim milk powder in the cage, the

newly emerged flies were given 35 g of liver every day for one hour to provide protein to the females for egg production (Mackerras 1933).

Fitness Measures Verification of *Lucilia sericata*

To relate adult female body size to potential lifetime fecundity as a proxy of fitness, the number of eggs contained within a females' ovaries can be related to how many oviposition events can occur in its life span (Mackerras 1933). This methodology was based on Bennettova and Fraenkel (1981) that demonstrated that adult size depends on larval nutrition. Thirty five grams of liver in a petri dish was placed as an oviposition medium in the colony cage of *Lucilia sericata* for 12 h during light hours. Eggs were placed at 25ºC in a growth chamber until they hatched and then 1600 first instars were distributed equally into 4-500 mL mason jars containing beta chip wood shavings and sealed with a mason jar ring and landscape material to contain the larvae but allow for air flow into the jar. Four mason jars were used with two of the mason jars were given approximately 15 g of pork liver and the other two jars were given approximately 35 g of liver in order to obtain a range of sizes of adults. A range of adult sizes was important to obtain egg numbers not only from the average size adults but also to see if very small females produce a smaller number of eggs. Larvae in the 35 g of liver treatment jars were supplied with additional excess liver until they left the food to pupate. Larvae in the 15 g of liver treatment jars were not fed any additional liver during the remainder of their development to ensure small, undersized adults. When all the larvae had left the food, the liver was removed and additional dry beta chips were added to each jar to promote pupation.

Adults from all four of the jars were released into a single cage for over 24 h. The adults were supplied with water, sugar and skim milk powder as needed in the cage. Liver was supplied as a protein meal for egg development for 2 h/day for 5 d. Six days after emergence, females were visibly gravid with swollen abdomens and the cage was placed into a -20ºC freezer for 6 h to kill all the flies.

Fifty females were then selected with a range of sizes from large to small across all available sizes. Once selected, each fly was assigned a number from 1 to 50. Wing, tibia and thorax length was measured for each individual under an ocular micrometer. After measurement, the ovaries were extracted using two pairs of forceps to open the abdomen and remove both ovaries intact while keeping the adult female submerged in 70% ethanol. The ovaries were stored in 70% ethanol in 0.75mL vials with caps until counting.

Egg counts were performed in petri dishes flooded with 70% ethanol under a dissecting stereoscopic microscope. Each ovary was separated and the mature eggs were counted individually. The total number of eggs was recorded for each female. If the eggs in the ovaries were not large enough to count, due to immaturity of the eggs, that female was discarded from the counts.

Larval Experiments

A pilot study was conducted in order to determine larval densities for this experiment. In order to create an environment with a limited food resource, the amount of resource that larvae consume is important. Trials with 200 and 400 individual larvae of *L. sericata* were conducted using rats weighing 500 g-700 g. Three replicates were completed and the mean larval consumption was 0.5g/ larva from the first instar stage

until pupation. These results showed that for a community of 300 individuals, the food resource provided should weigh less than 150 g to create an environment with a limited resource. Using these results, food resources provided for the larvae in the study weighed 125 g $\pm$ 20 g in each community created and five complete replicates of the thirty five jars were completed.

Community compositions were chosen based on previous undergraduate work (Reid unpublished 2009), natural communities observed in this region (Rosati and VanLaerhoven 2007), and observations in the field (Wells and Greenberg 1994). The single species communities were constructed to create a baseline development time, mortality, and adult size on different resources for each of the three species. Development times of the single species could also be used to compare other development studies done under similar lab conditions. Different cohorts of individuals were used for each of the five replicates. The community of 1:1:2 contained 75 individuals of both *P. regina* and *L. sericata* and 150 *C. rufifacies* individuals. This was chosen based on observations that *C. rufifacies* has been observed to outnumber non-predacious species on carrion resources by occupying up to 90% of the total blow flies on carrion baits in the field (Baumgartner 1993) but have not been widely studied in the lab (Wells and Greenberg 1992). The communities of 2:1:1, 1:2:1, and 1:1:1 were selected based on undergraduate work showing that when *L. sericata* and *P. regina* are reared together, *L. sericata* acts as a facilitator for *P. regina* when reared on pork liver, but this interaction was not seen on the pork muscle. The effects of this facilitation by *L. sericata* differed based on the abundance of each of these two species. The three communities were chosen for this

study to see if the facilitation of *P. regina* was still evident with an omnivore present
(Table 1).

Food resources for this laboratory experiment were chosen based on previous
research that demonstrated that different tissue types change the duration of development.
Pork liver, pork muscle, beef liver, beef muscle, and whole rat were selected for this
experiment. Clark *et al* (2006), Day and Wallman (2006), and Ireland and Turner (2006)
compared different organs and tissues across a variety of Calliphoridae showing that
development changed based on resource type, but this was only studied in single species
environments. Based on previous work done by Wells and Greenburg (1992), freezing
the resource before use did not affect the larval feeding behaviour. In order to minimize
variation between replicates, each of the 5 resources were purchased at the same time and
cut into the respective weights and placed into a -20ºC freezer. Samples of the carrion
food resources were also sent for nutritional analysis (Table 2).

Larval Development Time and Duration

Development was measured every 6 h (0300 h, 0900 h, 1500 h, 2100 h) and the
instar stage recorded within each jar. In the mixed community jars, stage of development
between the three species was recorded as the same during the early instars due to the
difficulty in distinguishing between the three species. As the larvae reached the later third
instar stage, development of individual species were recorded. When the wandering stage
began as indicated by the 3rd instar larvae leaving the food resource in search of a
pupation site, the shavings were checked for pupae during the developmental checks.
Once they began to pupate, development checks were reduced to once every 12 h (0900h

Table 1. Experimental set up for one replicate which contains 35 experimental jars. Each treatment consists of 300 individuals with the mixed ratios order '*P. regina: L. sericata: C. rufifacies*' with 1:1:1 representing 100 of each of the three species and the ratio 1:2:1 representing 75 *P. regina*, 150 *L. sericata*, and 75 *C. rufifacies* in one experimental community on each of the resources (pork liver and muscle, beef liver and muscle, and whole rat) used.

Resource Type	Pork Liver	Pork Muscle	Beef Liver	Beef Muscle	Whole Rat
Community Composition	1:1:1	1:1:1	1:1:1	1:1:1	1:1:1
	1:2:1	1:2:1	1:2:1	1:2:1	1:2:1
	1:1:2	1:1:2	1:1:2	1:1:2	1:1:2
	2:1:1	2:1:1	2:1:1	2:1:1	2:1:1
	P. regina only	*P. regina* only	*P. regina* only	*P. regina* only	*P. regina* only
	L. sericata only	*L. sericata* only	*L. sericata* only	*L. sericata* only	*L. sericata* only
	C. rufifacies only	*C. rufifacies* only	*C. rufifacies* only	*C. rufifacies* only	*C. rufifacies* only

* 300 individuals/ jar

Table 2. Nutritional composition of the resource types used in the experiment. The 35 g resources from each of the 5 replicates were obtained from the same initial source for each of the different carrion foods.

Ingredients		Pork Liver	Pork Muscle	Beef Liver	Beef Muscle	Whole Rat
Main components	Water	73.1	70.2	69.7	68.5	71.9
/100g of diet (g)	Proteins	20.8	19.6	20.8	20.1	16.4
	Fats	3.2	9.2	2.9	8.0	7.6
	Carbohydrates	1.0	-*	4.0	2.6	2.7

*no significant amount detected

and 2100h) to minimize disturbance to the wandering larvae in that particular jar as disturbance at this point may delay pupation (personal observation). At each 12 h interval, pupae were removed from the jars and put into petri dishes, observed daily at 0900 h for emergence. Time of emergence and sex of emerging flies was recorded.

All development times were then converted to accumulated degree hours (ADH) to eliminate any variation between treatments due to temperature variation. Accumulated degree hours were calculated with the temperature data taken every 6 h from a temperature data logger (ACR Systems Inc, SmartButton).

Fitness Measurements

When adults emerged, they were sorted by species, sex and treatment. The number of adults of each sex, the number of dead pupae, and the number adults that were not fully emerged was recorded. Adults were randomly selected from each jar for further measurements of their wing, tibia and thorax lengths. Many different measures have been used to represent adult body size in different studies including different wing vein lengths (Clark and Wall 2006; Smith and Wall 1997), adult dry weight (Shiao and Yeh 2008; MacKerras 1933), thorax length (Webber 1955), wing length (Rosa *et al* 2004; Stoffolano *et al* 2000), and tibia length (Rosa *et al* 2004). These three body measures were chosen based on previous studies. When possible there were 15 females of each species selected to be measured. If there were not enough adults for 15 of each species, all of the adult females of that species were measured. The wing was measured from the distal margin on the basicosta to the apex of the wing in a straight line. The thorax was measured on the midline from the proximal end near the head to the distal end of the scutellum. The tibia

was measured from the point of attachment to the femur to the attachment to the basitartus.

Mortality was calculated for the larval and pupal, stages as well as adults that did not fully emerge from their puparium. Larval mortality was represented as one measure per jar because it was not possible to distinguish between the species during the 2nd and early 3rd instar stages. Therefore, larval mortality was a calculation of the total number of larvae initially placed on the resource minus the total number of pupae recovered from the jar. Pupal mortality was a measure of the number of pupae that never produced an adult fly. Emergence mortality was calculated as the number of adults that did not fully emerge from the puparium or individuals that emerged but were unable to fully expand and harden their wings.

Statistical Analysis

The relationship between number of eggs and the three measures of body size as a proxy for fitness was examined using linear regression. Coefficient of variation was used to determine which of the three measures of body size best indicated female fecundity.

Experimental hours were converted into accumulated degree hours (ADH) to take temperature into account during development according to the following formula:

$$DH_1 = \text{Average temperature } (^{\circ}C)_{0\text{-}6h} \times 6\,h$$

$$DH_2 = DH_1 + \text{Average temperature } (^{\circ}C)_{6\text{-}12h} \times 6\,h$$

$$DH_3 = DH_2 + \text{Average temperature } (^{\circ}C)_{12\text{-}18h} \times 6\,h$$

$$DH_n = DH_{n\text{-}1} + \text{Average temperature } (^{\circ}C)_{18\text{-}24h} \times 6\,h$$

$$ADH = \Sigma\, DH_{1,\,2,\,\ldots\,n}$$

Duration of each development stage, minimum time to each stage, and mortality was analyzed using a Kruskal-Wallis analysis to determine differences between each of the community types. Each species was analyzed separately. This test was performed because the data was not normally distributed and could not be transformed into normal data, using log, ln, and square root functions, thus violating the assumptions for ANOVA analysis. A step-down step wise comparison was used to differentiate between the significantly different groups (Campbell and Skillings 1985). No difference was found between each of the resource types in the larval duration ($p > 0.05$) and development data ($p > 0.05$), therefore the resources types were pooled together for these analyses.

A linear mixed model analysis was used for the body measurements to test if there were differences in fitness due to the community compositions and basal resource type treatments. This test took into account the variation within an experimental jar when measuring multiple individuals from the same jar that were not independent from each other. Statistically significant results were determined by a p-value of ≤ 0.05.

RESULTS

Fitness Measures Verification

   Lucilia sericata had between 57 and 280 fully mature eggs within both ovaries

(mean= 178.31 $\pm$ 9.07, n=45). There was a positive correlation between the number of

eggs in each female and each of the adult female measures—wing (r^2=0.926, d.f. =43,

p<0.001), thorax (r^2=0.888, d.f. =43, p<0.001), and tibia (r^2=0.831, d.f. =43, p<0.001)

(Figure 1). The smallest female measured 1.4 mm tibia, 2.5 mm thorax, 4.7 mm wing

length while the largest female measured 2.5 mm tibia, 4.5 mm thorax, 7.9 mm wing

length. The mean size for each of the three body parts was 2.036 mm $\pm$ 0.048 mm for the

tibia, 3.738 mm $\pm$ 0.093 mm for the thorax, and 6.696 mm $\pm$ 0.15 mm for the wing

length. The coefficients of variation for each of the measures are as follows: 15.12% for

the wing length, 16.82% for the thorax length and 17.10 % for the tibia length.

Larval Development Time

   Phormia regina minimum development time to any of the measured life stages

was not affected by basal resource (p>0.05) or an interaction between resource and

community composition (p>0.05). The minimum time to the second instar larval stage

was not affected by community composition (p=0.457). However, the minimum time to

the third instar stage (H= 27.4247, d.f.=4, p<0.001), wandering (H= 49.289, d.f.=4,

p<0.001), and pupation (H= 11.323, d.f.=4, p=0.023) were affected by community

composition with the mixed species communities taking less time to reach each stage

compared to the single species communities (Figure 2).
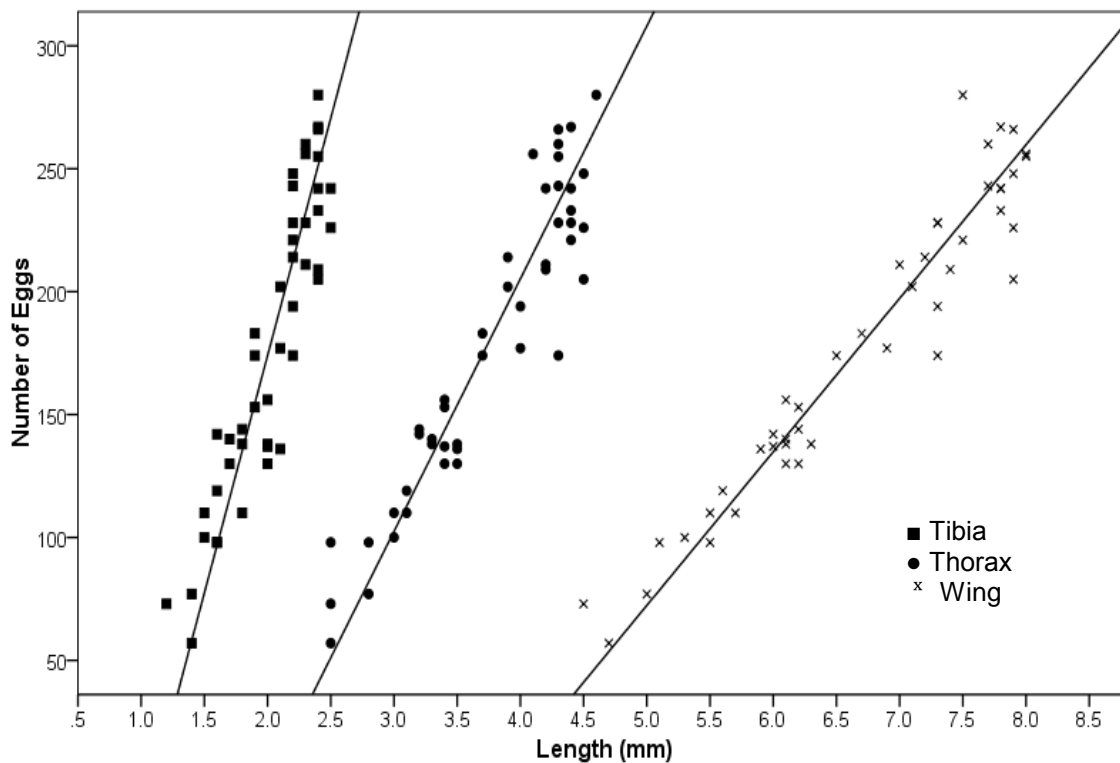
Figure 1. Relationship between egg production and adult female body size measures for *Lucilia sericata* reared on pork liver from first instar stage to adult. Each symbol represents an individual female measurement. Lines represents the linear regression; ■ – r^2=0.831, p<0.001, Y (number of eggs) = 160.503x − 146.262, Coefficient of variation=0.171; ● – r^2=0.888, p<0.001, Y= 57.866 x − 209.136, Coefficient of variation=0.168; ˣ – r^2=0.926, p<0.001, Y = 91.222x − 162.658, Coefficient of variation=0.152.
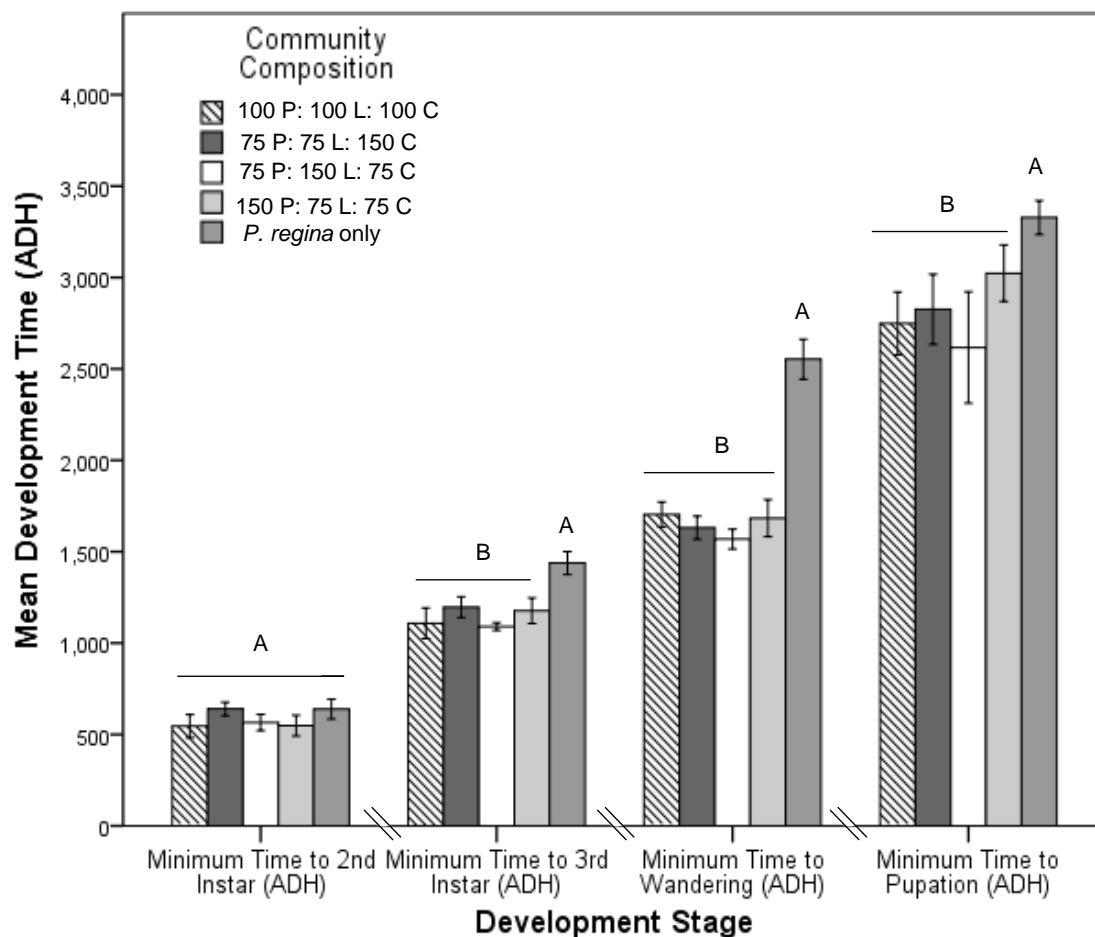
Figure 2. Effect of community composition on minimum development time (accumulated degree hours, ADH) of *Phormia regina* larvae. Minimum time was measured from egg eclosion to the minimum time to reach each of the development stages ± SE. Larvae were reared on pork liver, pork muscle, beef liver, beef muscle, and whole rat carrion food resources. Results from each of the resources types did not differ and were pooled together (p>0.05). Five replicates of each resource and community types were completed. Within each developmental stage, means followed by the same letter, as indicated by a line over the bars, did not differ (p>0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies.*

Similar to *P. regina*, *C. rufifacies* minimum development time to each of the life stages was not affected by the basal resource type (p>0.05) or an interaction between resource and community composition (p>0.05). The minimum time to second instar was also not affected by the community composition (p=0.896). However, the minimum time to the third instar stage (H= 10.037, d.f.=4, p=0.040), wandering (H= 25.932, d.f.=4, p<0.001), and pupation (H= 12.538, d.f.=4, p=0.014) were affected by community composition, demonstrating that within the mixed species communities, *C. rufifacies* developed faster than when reared on its own (Figure 3).

Lucilia sericata minimum development time to each life stage was not affected by an interaction between resource and community composition (p>0.05) or basal resource type (p>0.05) with the exception of the wandering stage (H= 15.282, d.f. =4, p=0.004). *Lucilia sericata* reached the wandering stage in the shortest amount of time when reared on beef muscle and pork muscle and subsequently the slowest on beef liver. With respect to community composition, the minimum time to both second (p=0.839) and third (p=0.477) instar stages were not affected. Conversely, *L. sericata*'s minimum time to wandering (H=25.262, d.f. =4, p<0.001) and to pupation (H=12.706, d.f. =4, p=0.013) were affect by community composition where its development was slowest when reared in the single species community and faster when reared within the mixed communities (Figure 4).

Duration of Development Stage

Phormia regina duration of each of the life stages measured was not affected by the basal resource type (p>0.05) or an interaction between resource and community composition (p>0.05). However, the duration of the second instar (H= 15.46, d.f.= 4,
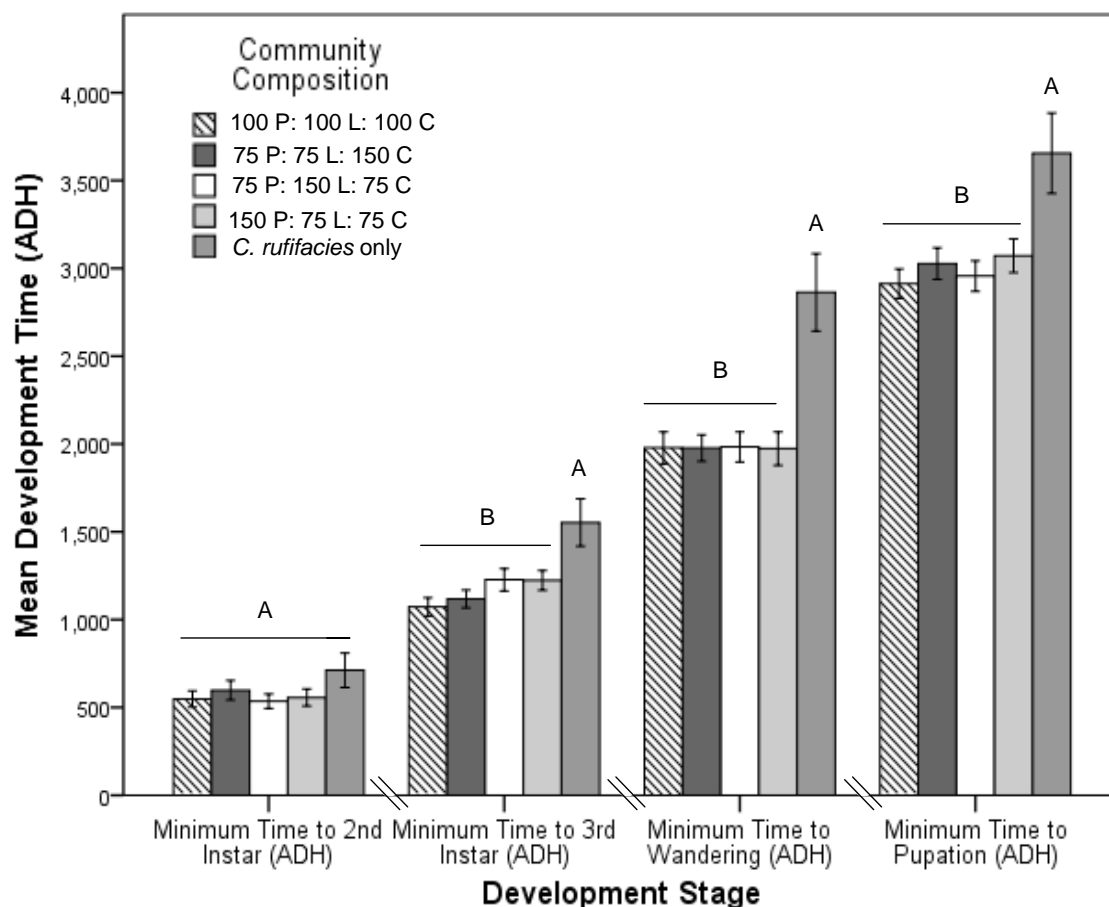
Figure 3. Effect of community composition on minimum development time (accumulated degree hours, ADH) of *Chrysomya rufifacies* larvae. Minimum time was measured from egg eclosion to the minimum time to reach each of the development stages $\pm$ SE. Larvae were reared on pork liver, pork muscle, beef liver, beef muscle, and whole rat carrion food resources. Results from each of the resources types did not differ and were pooled together ($p>0.05$). Five replicates of each resource and community types were completed. Within each developmental stage, means followed by the same letter, as indicated by a line over the bars, did not differ ($p>0.05$). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies*.
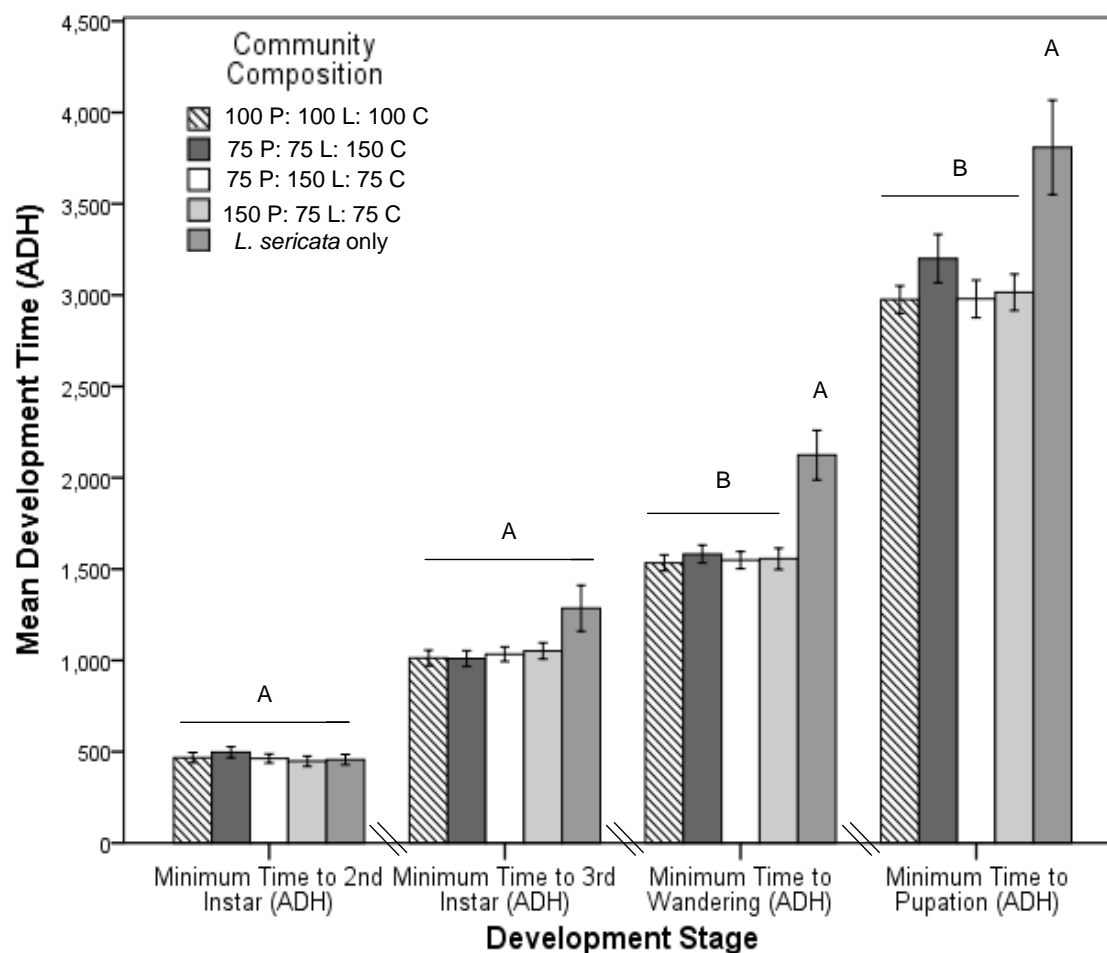
Figure 4. Effect of community composition on minimum development time (accumulated degree hours, ADH) of *Lucilia sericata* larvae. Minimum time was measured from egg eclosion to the minimum time to reach each of the development stages $\pm$ SE. Larvae were reared on pork liver, pork muscle, beef liver, beef muscle, and whole rat carrion food resources. Results from each of the resources types did not differ and were pooled together (p>0.05). Five replicates of each resource and community types were completed. Within each developmental stage, means followed by the same letter, as indicated by a line over the bars, did not differ (p>0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies.*

p=0.004), third instar (H=14.812, d.f.=4, p=0.005), wandering (H=32.105, d.f.=4, p<0.001), pupal (H= 43.12, d.f.=4, p<0.001), and emergence (H=18.512, d.f.=4, p=0.001) stages were affected by the community composition. The longest duration time in each stage occurred when *P. regina* was reared in the single species environment. Within the mixed species communities, when there was a difference among the mixed communities it usually occurred in the 1:1:1 species mix with this composition having the shortest duration (Table 3).

     Chrysomya rufifacies duration of each life stage was not affected by basal resource type (p>0.05) with the exception of the wandering and pupal stages. The wandering stage (H=19.070, d.f.=4, p=0.001) was affected by resource type with larva reared on the whole rat having the shortest duration and beef liver taking the longest for all of the larvae to transition to the next stage. The pupal stage (H=13.727, d.f.=4, p=0.008) was similar to the wandering stage with the shortest duration observed on the whole rat and the longest duration for all of the larvae to pupate was on the beef liver and pork muscle. Looking at the effect of community composition on the duration of each stage, there was a difference in the second instar (H=10.132, d.f.=4, p=0.038), third instar (H=13.776, d.f.=4, p=0.008), pupal (H=19.583, d.f.=4, p=0.001) and emergence (H=10.615, d.f.=4, p=0.031) stages. Although the difference between the mixed and single species communities was not clearly defined, the single species communities usually had longer stage duration than the mixed communities but this was not always the case (Table 3).

     Lucilia sericata life stage durations were not affected by the basal resource type (p>0.05) that the larvae fed upon or an interaction between resource and community

Table 3. Duration of each larval stage measured from the first individual reaching the stage to the last individual leaving the stage. Larvae were reared on pork liver, pork muscle, beef liver, beef muscle, and whole rat but results from each were pooled because there was no significant difference between the food types (p>0.065). Means within columns for each species followed by the same letter did not differ (p>0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies*.

		Duration of 2nd Instar Stage (ADH)	Duration of 3rd Instar Stage (ADH)	Duration of Wandering Stage (ADH)	Duration of Pupal Stage (ADH)	Duration of Emergence Stage (ADH)
		Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE
P. regina	100 P: 100 L: 100 C	982.07 ± 67.62 [b]	1936.58 ± 148.51 [b]	1116.63 ± 117.22 [c]	54.67 ± 36.19 [c]	
	75 P: 75 L: 150 C	1018.66 ± 68.05 [b]	1839.17 ± 156.34 [b]	1743.17 ± 365.21 [bc]	228.00 ± 125.04 [bc]	443.25 ± 257.33 [b]
	75 P: 150 L: 75 C	964.82 ± 68.10 [b]	1807.27 ± 128.04 [b]	1395.50 ± 335.56 [bc]	371.90 ± 166.46 [bc]	486.19 ± 332.08 [b]
	150 P: 75 L: 75 C	1043.19 ± 74.13 [b]	1702.79 ± 117.89 [b]	1772.75 ± 147.95 [b]	633.24 ± 182.79 [b]	544.92 ± 171.19 [b]
	P. regina only	1323.56 ± 72.04 [a]	2396.98 ± 111.98 [a]	2575.27 ± 143.31 [a]	1778.80 ± 121.51 [a]	1445.93 ± 186.55 [a]
C. rufifacies	100 P: 100 L: 100 C	1007.69 ± 62.47 [b]	2420.24 ± 138.36 [ab]	2034.08 ± 103.72	1099.08 ± 82.55 [b]	1353.08 ± 208.82 [ab]
	75 P: 75 L: 150 C	1029.51 ± 71.22 [ab]	2156.92 ± 157.09 [b]	2289.08 ± 116.67	1314.79 ± 117.40 [ab]	1376.00 ± 178.41 [b]
	75 P: 150 L: 75 C	1008.49 ± 62.84 [b]	2099.21 ± 121.69 [b]	2002.91 ± 102.56	999.55 ± 75.63 [b]	969.75 ± 153.31 [ab]
	150 P: 75 L: 75 C	1082.80 ± 77.36 [ab]	2190.45 ± 111.20 [b]	2210.51 ± 114.82	1155.77 ± 101.08 [b]	1449.84 ± 153.32 [ab]
	C. rufifacies only	1419.32 ± 119.00 [a]	2832.37 ± 171.27 [a]	2581.78 ± 204.01	1705.53 ± 148.52 [a]	1795.31 ± 218.45 [a]
L. sericata	100 P: 100 L: 100 C	999.3 ± 65.77	1755.35 ± 154.80	3112.82 ± 223.50 [b]	1644.71 ± 211.99 [bc]	1664.72 ± 244.67
	75 P: 75 L: 150 C	1023.40 ± 65.96	1684.60 ± 143.79	3037.21 ± 139.13 [b]	1375.44 ± 152.04 [c]	1862.82 ± 242.16
	75 P: 150 L: 75 C	998.49 ± 63.27	1704.15 ± 136.00	3354.81 ± 129.06 [b]	1846.57 ± 119.73 [b]	2040.05 ± 254.88
	150 P: 75 L: 75 C	1070.02 ± 66.86	1689.47 ± 128.09	3133.96 ± 135.72 [b]	1551.76 ± 135.59 [bc]	1971.25 ± 215.43
	L. sericata only	1272.77 ± 124.40	2086.06 ± 107.56	8056.38 ± 1076.80 [a]	4699.36 ± 736.84 [a]	2880.83 ± 308.30

composition (p>0.05). The only stages that were affected by community composition were the length of the wandering (H= 33.973, d.f. =4, p<0.001) and pupal (H=38.743, d.f. =4, p<0.001) stages. When *L. sericata* was reared in the single species communities, the larva wandered longer than the mixed communities in the same stage. A similar trend was observed in the amount of time it took for all of the larvae in the single species community to pupate as opposed to the mixed communities where they initiated pupation much faster and remained in the pupal stage for a shorter amount of time (Table 3).

Fitness Measures

Phormia regina adult fitness was affected by community composition. Tibia length was not affected by an interaction between resource and community composition ($F_{11, 454}$=1.378, p<0.18). Tibia length was affected by community composition ($F_{4, 454}$=9.174, p<0.001) leading to larger tibias when *P. regina* was reared in single species communities. The smallest tibias were measured from individuals in a mixed community composition with the other two species. Wing length ($F_{4, 454}$=17.168, p<0.001) (Figure 5) and thorax length ($F_{4, 454}$=7.822, p<0.001) responded similarly to tibia length which was expected based on the egg experiment done with *L. sericata*. Resource type did not affect adult female size (p>0.05).

Chrysomya rufifacies adult fitness was affected by an interaction between community composition and resource type. The tibia measurements were larger ($F_{16, 1782}$=2.522, p<0.001) when *C. rufifacies* was in the mixed communities at either equal or lesser number individuals than the other two species. Within a community type, the adult tibias were larger when the larvae fed on whole rat. Wing ($F_{16,1782}$=3.288, p<0.001)

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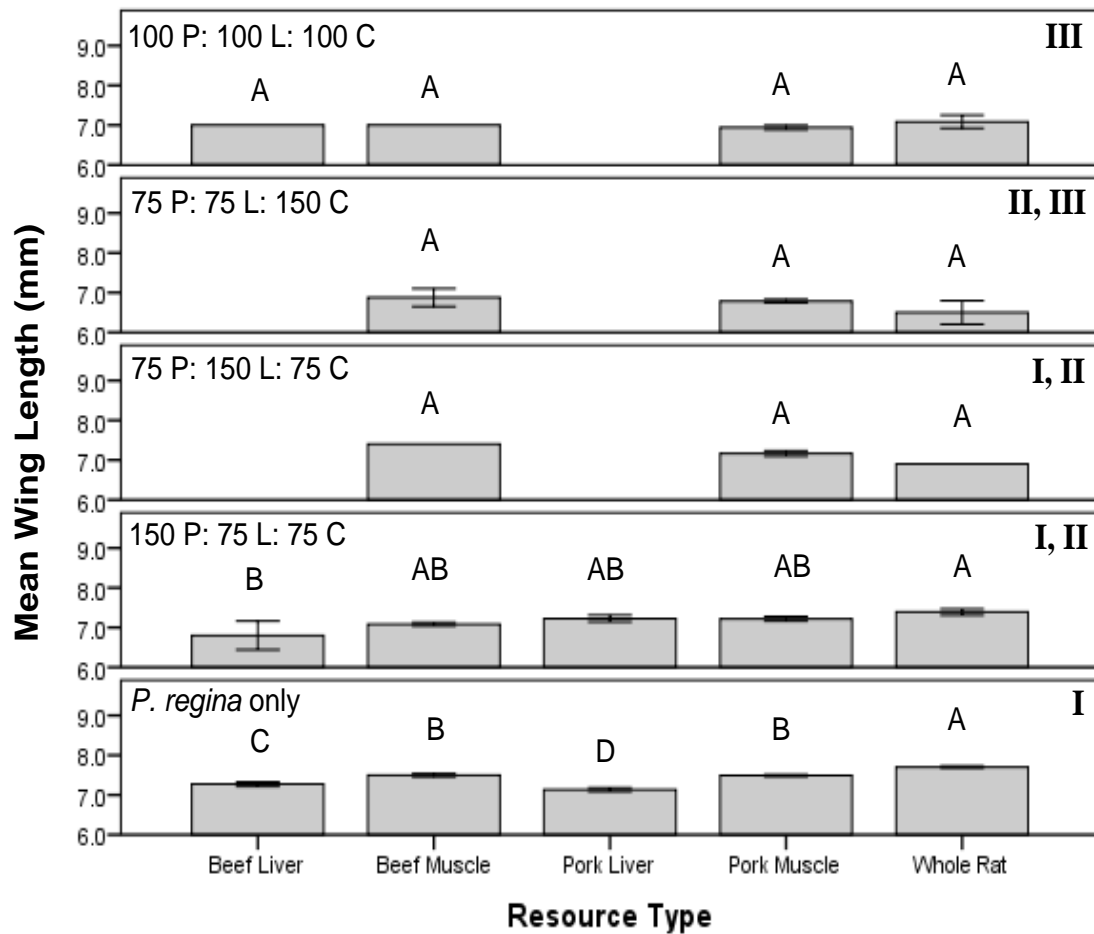
Figure 5. Mean wing length (mm) of adult *Phormia regina* females reared from each carrion food resource type and the different blow fly community compositions. Five replicates of each resource and community composition type were completed. Within each community composition type, means followed by the same later did not differ (p>0.05). Between community types, means followed by the same Roman numeral did not differ (p>0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies*.

(Figure 6) and thorax ($F_{16,1782}$=3.517, p<0.001) lengths demonstrated similar results as tibia lengths with length being longer when there are fewer *C. rufifacies* in the community than *L. sericata* or *P. regina*. Wing and thorax lengths were also longer when the larvae fed on whole rat.

Lucilia sericata adult fitness was affected by an interaction of resource and community composition. Tibia length was ($F_{4, 1315}$=3.381, p<0.001) longer when *L. sericata* was reared in a single species community. An interaction between community composition and resource type also affected both wing ($F_{16, 1315}$=4.705, p<0.001) (Figure 7) and thorax ($F_{16, 1315}$=2.956, p<0.001) length. Measures were larger when *L. sericata* was reared on its own in the single species communities. When there was a difference between the resource types, rat, beef liver, and pork liver produced the largest measure when *L. sericata* dominated in the 1:2:1 community composition but these individuals were smaller overall compared to the other community compositions. When the community contained equal numbers of all species, the 1:1:1 community, *L. sericata* was largest on rat and beef muscle but again individuals were smaller overall when compared to the other communities.

Mortality

Community composition influenced larval mortality of both *P. regina* (H=77.527, d.f. =4, p<0.001) (Figure 8) and *L. sericata* (H=44.716, d.f. =4, p<0.001) (Figure 9) with mortality being lower when each species was reared on its own. Pupal mortality was also influenced by community composition showing a similar pattern as larval mortality. Both *P. regina* (H=38.723, d.f. =4, p<0.001) (Figure 10) and *L. sericata* (H=12.091, d.f. =4,

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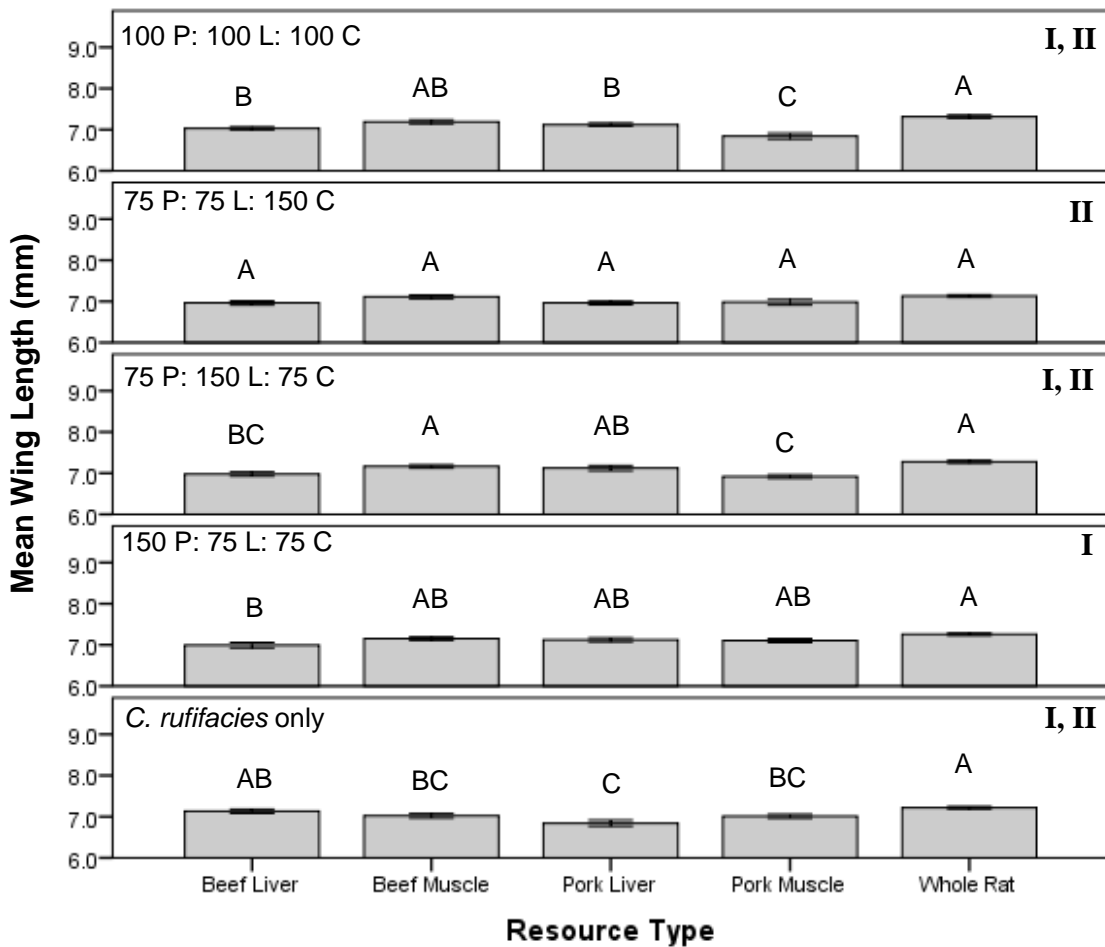
Figure 6. Mean wing length (mm) of adult *Chrysomya rufifacies* females reared from each carrion food resource type and the different blow fly community compositions. Five replicates of each resource and community composition type were completed. Within each community composition type, means followed by the same later did not differ (p>0.05). Between community types, means followed by the same Roman numeral did not differ (p>0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies*.
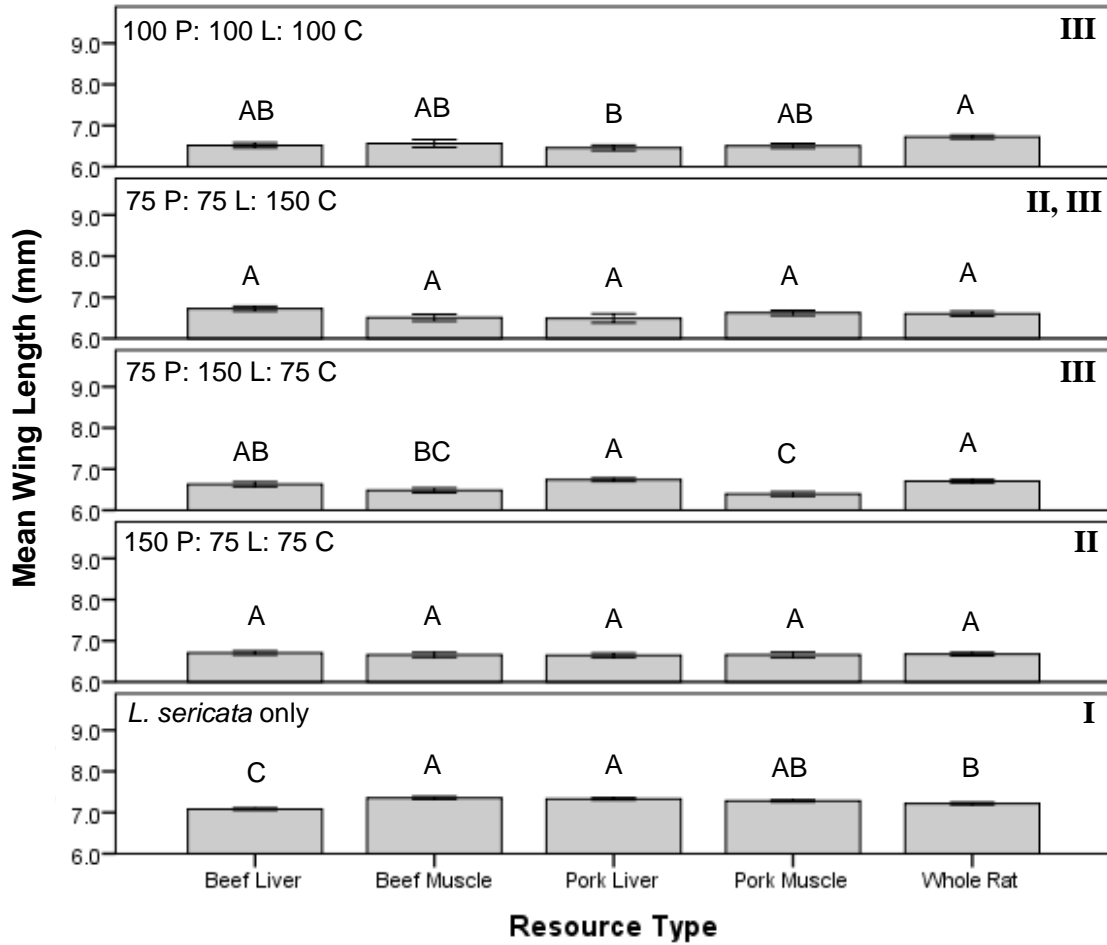
Figure 7. Mean wing length (mm) of adult *Lucilia sericata* females reared from each carrion food resource type and the different blow fly community compositions. Five replicates of each resource and community composition type were completed. Within each community composition type, means followed by the same later did not differ (p>0.05). Between community types, means followed by the same Roman numeral did not differ (p>0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies.*
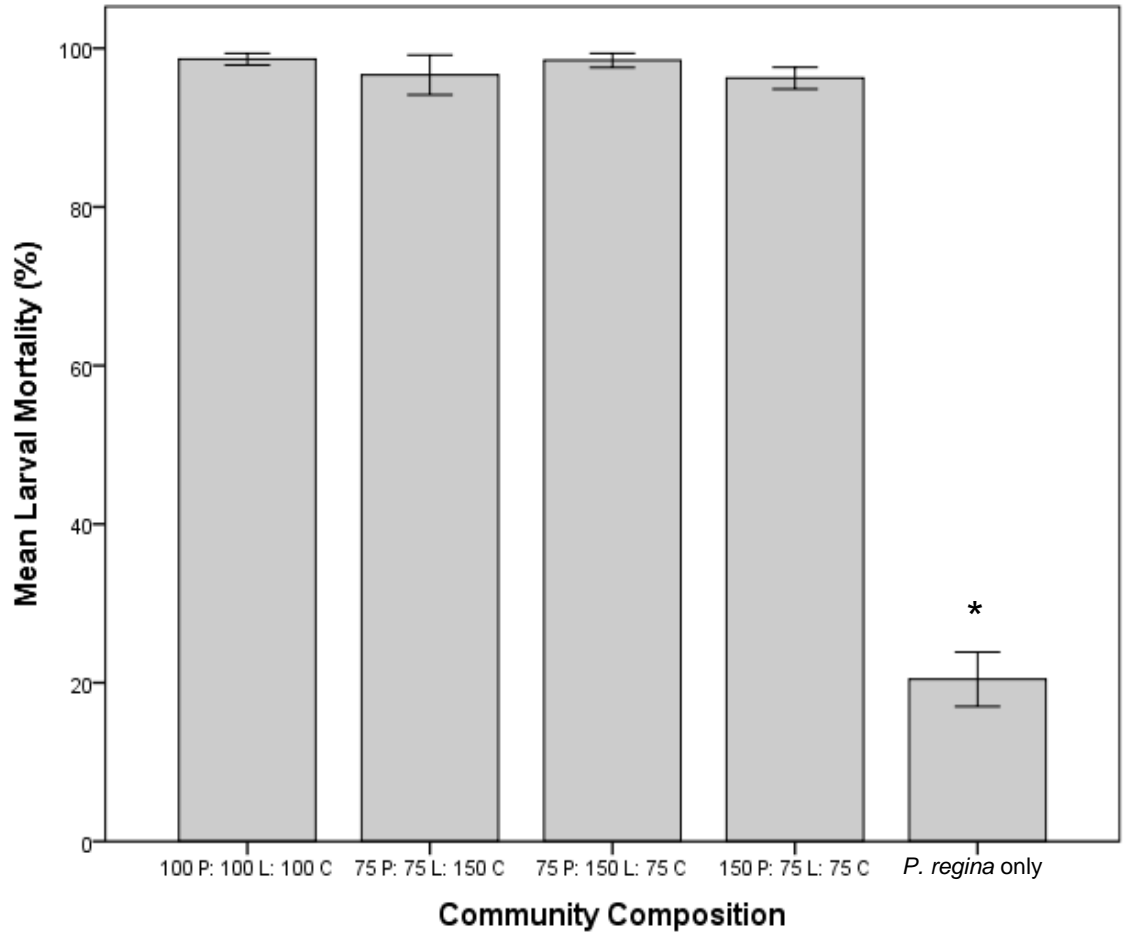
Figure 8. Mean larval mortality (% larval death $\pm$ SE) of *Phormia regina* within different blow fly community compositions (H=77.527, d.f=4, p<0.001). Larval mortality was measured as the number of individuals that died from first instar to pupation. Larvae were reared upon pork liver, pork muscle, beef liver, beef muscle, and whole rat carrion food resources but results from each of the resources types did not differ and were pooled together (p>0.05). Five replicates of each resource and community types were completed. Means indicated by an asterisk differ from means without an asterisk (p<0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies*.
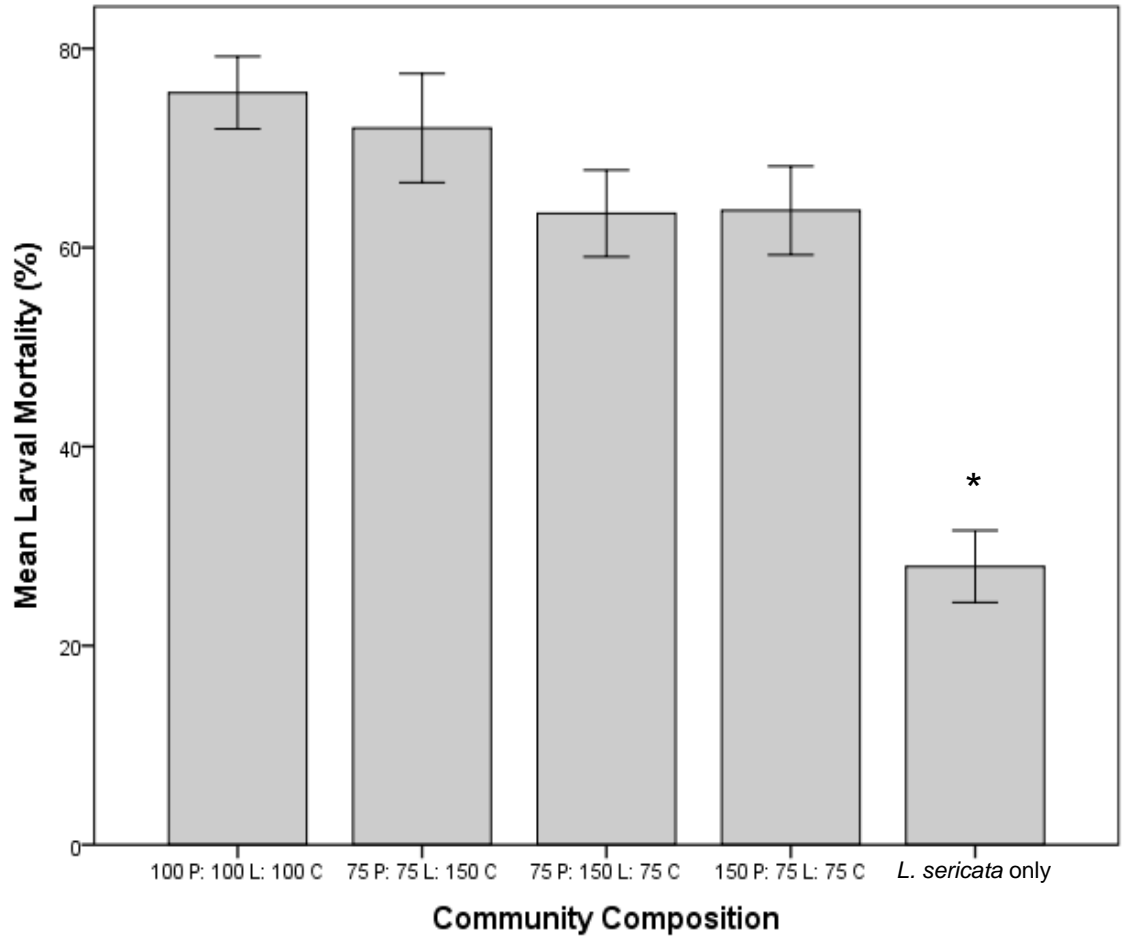
Figure 9. Mean larval mortality (% larval death $\pm$ SE) of *Lucilia sericata* in different community compositions (H=44.716, d.f=4, p<0.001). Larval mortality was measured as the number of individual deaths from first instar to pupation. Larvae were reared upon pork liver, pork muscle, beef liver, beef muscle, and whole rat. Results from each of the resources types were not significantly different and were pooled together (p>0.05). Five replicates of each resource and community types were completed. Means indicated by an asterisk differ from means without an asterisk (p<0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies.*

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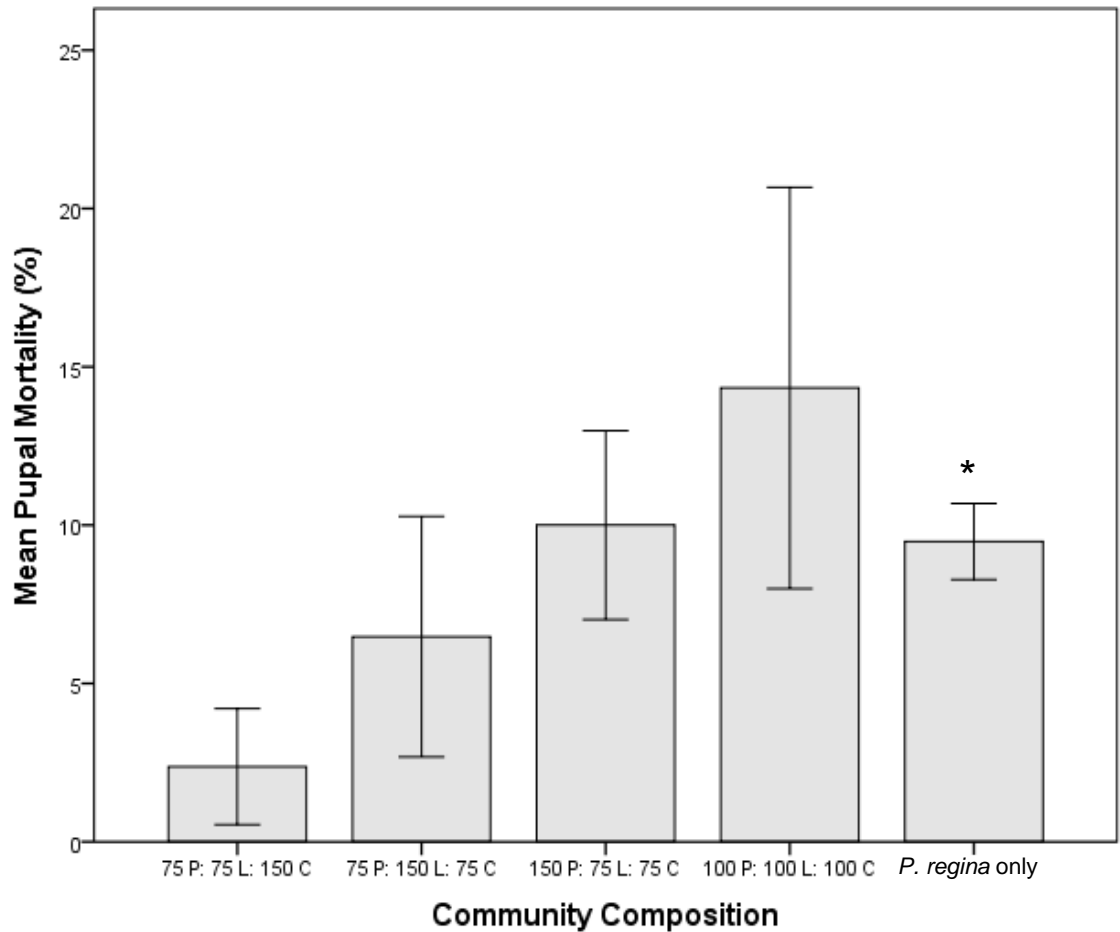
Figure 10. Mean pupal mortality (% pupal death $\pm$ SE) of *Phormia regina* within different blow fly community compositions (H=38.723, d.f=4, p<0.001). Pupal mortality was measured as the percent of pupae that did not emerge as adults. Larvae were reared until pupation on pork liver, pork muscle, beef liver, beef muscle, and whole rat carrion food resources but results from each of the resources types did not differ and were pooled together (p>0.05). Five replicates of each resource and community types were completed. Means indicated by an asterisk differ from means without an asterisk (p<0.05). P-*Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies*.

p<0.05) (Figure 11) had a lower pupal mortality when reared on its own. Emergence mortality was not influenced by community composition for either species (p>0.05).

There was no effect of resource on larval (p>0.05), pupal (p>0.05) or emergence (p>0.05) mortality with respect to any of the three species. *Chrysomya rufifacies* mortality was not influenced by community composition or basal resource type (p>0.05).
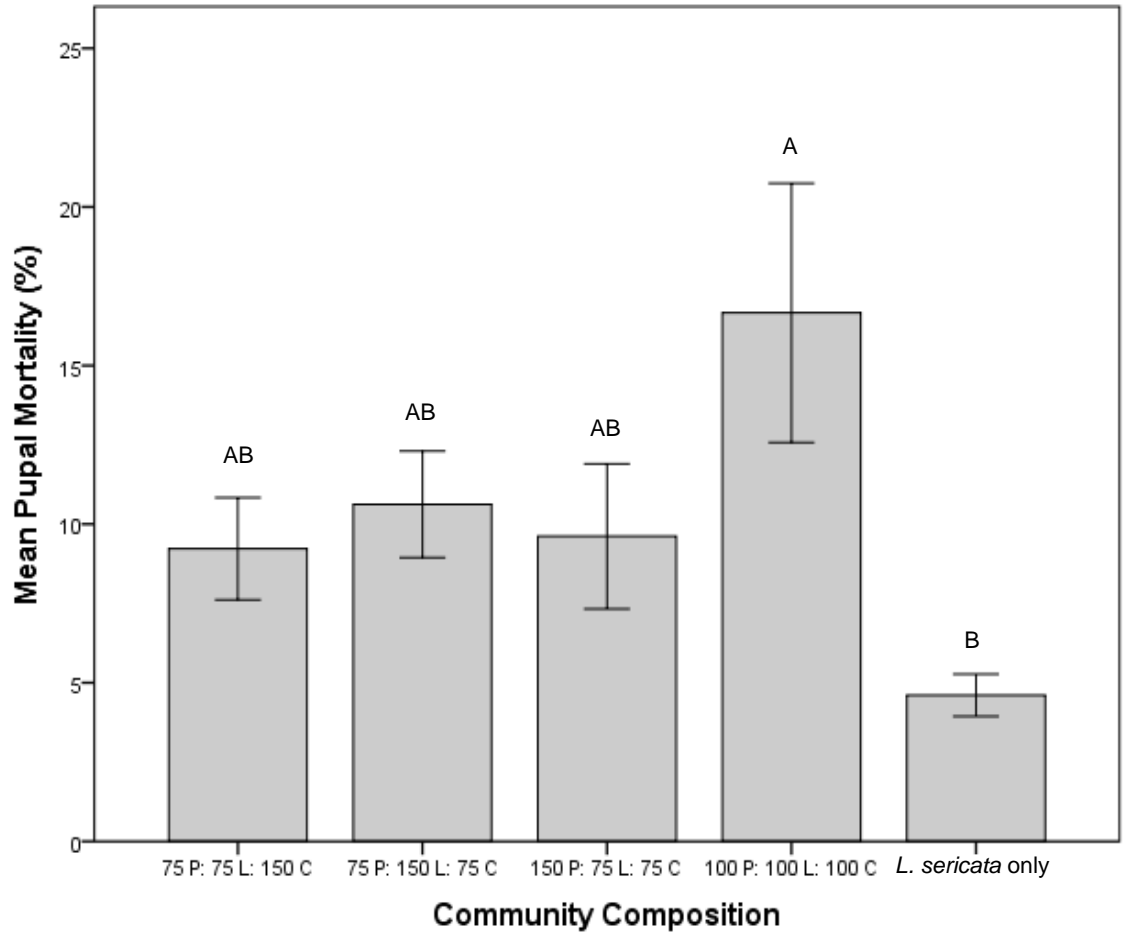
Figure 11. Mean pupal mortality (% pupal death $\pm$ SE) of *Lucilia sericata* within different blow fly community compositions (H=12.091, d.f=4, p<0.05). Pupal mortality was measured as the percent of pupae that did not emerge as adults. Larvae were reared until pupation on pork liver, pork muscle, beef liver, beef muscle, and whole rat carrion food resources but results from each of the resources types did not differ and were pooled together (p>0.05). Five replicates of each resource and community types were completed. Means followed by the same letter did not differ (p>0.05). P- *Phormia regina*, L- *Lucilia sericata*, C- *Chrysomya rufifacies*.

DISCUSSION

In my study I determined that, with respect to *L. sericata,* the number of eggs in a fecund female best correlated with the length of the female's wing and I was able to correlate these measures to overall fitness. Secondly, developmental plasticity occurred in the multispecies communities resulting in faster development times and shorter duration at each developmental stage when compared to the single species communities. Lastly, the fitness of each species was affected by resource type and community composition where *L. sericata* and *P. regina* showed a decrease in fitness and an increase in mortality in the mixed species communities as compared to each species reared on its own. *Chrysomya rufifacies* mortality however was not affected by the community composition or the basal resource type.

Fitness Measure Verification

My study validated the use of tibia, wing, and thorax measurements as fitness indicators by showing a strong positive relationship between initial female fecundity and body size measures for *L. sericata*. Mackerras (1933) demonstrated that a mating pair of *L. sericata* allowed an individual female to have 13 oviposition events within its lifetime of 77 days, with an average of 183 eggs per event. Although no measures of the females used in Mackerras (1933) study were taken, my study found the female's ovaries, on average, contained similar numbers of eggs. Wing vein length was found to have the lowest coefficient of variation and can be used to extrapolate the offspring potential of an individual female under each different community and resource studied. My findings also demonstrate that counting the number of eggs contained within the ovaries can be used in

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place of isolating a mating pair and waiting for oviposition to occur to observe potential fecundity.

The concept of larger individuals producing more eggs is not a novel concept (VanLaerhoven and Stephen 2003) and egg numbers have been recorded for many species including *Eucalliphora lilaea* (Walker) (Diptera: Calliphoridae)*, L. sericata*, *C. rufifacies* and *Cynomyopsis cadaverina* (Robineau-Desvoidy) (Diptera: Calliphoridae) (Kamal 1958; Mackerras 1933, Roy and Siddones 1939). However, there has not been a study to date that correlated body measurements, including dry weight, specific wing vein length, or other body measure, to the number of eggs found within blow fly females (Shiao and Yeh 2008; Prinkkila and Hanski 1995; Clark *et al* 2006; Ireland and Turner 2006; Mackerras 1933), although this effect has been shown in other taxa (VanLaerhoven and Stephen 2003; Khafagi *et al* 2011). My study was able to conclusively state that the body size measures used in this experiment correlate to initial fecundity for *L. sericata*.

Larval Development & Stage Duration

My research has demonstrated the influence of community composition and basal resource on the development rate of blow flies. Although not all development stages were affected for the species in my study, it has been shown in other studies that the resource that the larvae feed upon can influence development time. Clark *et al* (2006) showed that among organ types of both bovine and swine, there was a difference in development time of *L. sericata*. Among the organs used, those fed beef or pork liver developed the slowest. Similar studies (Day and Wallman 2006; Kaneshrajah and Turner 2004) also demonstrated that among organ types from different animals, the larvae reared on liver

had the slower development rates. Ireland and Turner (2005) compared not only liver and brain, but also pork muscle. The nutritional analysis on the liver and muscle were similar to the tissues used in my study and demonstrated that although development time changed between different larval densities, the larvae of *Calliphora vomitoria* (Robineau-Desvoidy) (Diptera: Calliphoridae) reared on liver developed faster than those fed the pork muscle in Ireland and Turner's (2005) study. Although there are varying results on tissue type influencing development rates, my study did not conclusively demonstrate that basal food resource type directly influences development in terms of length of development.

Shiao and Yeh (2008) looked at interactions between *C. rufifacies* and *Chrysomya megacephala* (Fabricius) (Diptera: Calliphoridae), a non-predacious species, and showed that where the two species are present, *C. rufifacies* had a shorter duration of its second instar stage. This could be due to its predatory stage beginning during the second and third instar stages or its behaviour to invade a heterospecific's feeding mass to acquire its food resource more easily (Shiao and Yeh 2008). This effect was observed during my study as the duration of the developing larvae was increased by the absence of other species present in the community.

When comparing the single species data to available data sets for these species (Byrd and Butler 1997; Byrd and Allen 2001; Grassberger and Reiter 2001; Melvin 1934), my data fit within the accepted development times. Because my data started from the first instar stage, the time from oviposition to egg eclosion was accounted for by adding this missing time interval from published papers to allow for development

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comparison to known data (Byrd and Butler 1997; Byrd and Allen 2001; Grassberger and

Reiter 2001; Melvin 1934). In comparison to Kamal (1958) and Byrd and Allen (2001),

the development of *P. regina* within the single species communities agrees with their

developmental data. For example, Byrd and Allen (2001) show a range for time to

pupation of 3350-7100 ADH. My data fall within this range for the single species data

but the mixed species data is shorter by a maximum of 413 ADH. My data do not agree

with the developmental data from Marchenko (2001) on time to pupation of *P. regina*

which showed that it took longer to pupate when compared to my study, 4440 ADH

compared to 3647.92 ADH. The discrepancies between my study and previously

published studies could be attributed to the disturbance while *P. regina* was feeding by

the other two species present and may reflect the time for the individuals to return to

feeding if they wandered from the food prematurely.

  Chrysomya rufifacies development in the single species communities agreed with

Byrd and Butler (1997) development data for time to pupation giving a range from 3350-

4050 ADH. Comparing the development time to pupation of the mixed communities to

Byrd and Butler (1997), my data did not agree with *C. rufifacies* time to pupation with

this study's data falling short of the range by a maximum of 438 ADH. Similar findings

were demonstrated in the minimum time to emergence with the single species community

falling into Byrd and Butler's (1997) range of 5925-7225 ADH while the mixed species

communities fell short by a maximum of 183 ADH. As determined in my lab study, *C.*

rufifacies was unaffected by the resource type but, as a facultative predator and an

omnivore, the presence of other species to feed upon may attribute to its accelerated development rate.

Lucilia sericata development showed similar results when compared to Kamal (1958) and Grassberger and Reiter (2001). My data fell within the range given in the two comparing studies however; when there was a significant difference between the mixed and single species communities the mixed community data for *L. sericata* in my study did not fall within the development range data. For example, according to Grassberger and Reiter (2001) development to the wandering or post feeding stage should take approximately 2376 ADH. This number is in the range of the minimum time to emergence found in my study, 2124.07 ± 135.14 ADH + 374 ADH for egg eclosion (Grassberger and Reiter 2001), however there is a discrepancy of at least 819 ADH when compared to the mixed species communities. This difference in development between the single and mixed communities may be attributed to the larvae wandering for a greater amount of time before pupating as a result of *C. rufifacies* disturbing the wandering larvae while trying to predate upon them.

Although I examined only three different species in a laboratory setting, the pattern of the change in larval development within mixed species communities could be an important tool when applying development data to calculate a post mortem interval (PMI) in forensic entomology. In examining the role of community composition on development within the environment created during my study, these interactions are causing a shorter time to complete development and consequently question the use of single species data to calculate PMI in situations where multiple species are present. This

does not mean that the current method of single species data is incorrect; however, more precise calculations could possibly be made in considering other species present in the community developing at the same time. The understanding that an individual or population of developing blow fly larvae are influenced by more than just temperature needs to be explored beyond just the species used in my study. My data suggests that interactions between populations of difference species changes the accepted development time from the single species data. This understanding could lead to narrower time estimates by accounting for accelerations in development not only by temperature, but by interactions between species. This further illustrates the need in forensic entomology to evaluate how interactions and communities dynamics effect calculations and conclusions they are able to draw from insect data.

Fitness & Mortality

My study has elucidated some complex interactions that occur within not only this specific community but within a community that contains an omnivore. *Lucilia sericata* showed increased mortality within these mixed species environments but was still able to develop into fit, viable adults. Its persistence within these specific communities may be due to attributes in the behaviour or morphology of this species. *Lucilia sericata* may survive in the mixed community compositions because when it is disturbed during feeding, the larvae were observed leaving the food and wandering away from the food source into the surrounding substrate, however; this was not quantified. Depending on the conditions, *L. sericata* may return to the resource to continue feeding and development. While this experiment was taking place, black blemishes were observed on the body of

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some the *L. sericata* that were wandering in the mixed communities. These were thought to be wounding however; to rule out fungal or bacterial contamination, *C. rufifacies* was starved for 12 hours and then placed into small petri dishes with *L. sericata*. The same blemishes were observed after *L. sericata* escaped *C. rufifacies* feeding. This escape may be due to a morphological feature that *L. sericata* possesses that allows it to escape. The wounding observed may be due to the small environment that the larvae were provided with for wandering. However, its behaviour to wander early and to escape predation by *C. rufifacies* may contribute to *L. sericata* persistence in these communities.

     Phormia regina did not have the same success in the mixed species communities as the other two species. After just one generation in these communities *P. regina* was driven to extinction. This competitive exclusion could be the result of very similar behaviour between *P. regina* and *C. rufifacies* in that both species remain on the food until pupation, frequently pupating on the resource and not leaving the resource in the post feeding stage to pupate in the surrounding substrate. Other species similar to *C. rufifacies* have also demonstrated the behaviour of remaining on or near the food source (Reigada and Godoy 2005). This behaviour by *P. regina* may provide *C. rufifacies* more opportunity to prey on the developing larvae. Since *P. regina* did not exhibit the early wandering behaviour of *L. sericata* when disturbed, the mortality of *P. regina* was nearly one hundred percent in the mixed environment. The lack of early wandering behaviour by *P. regina* is the opposite of Byrd and Allen's (2001) observations that *P. regina* wandered earlier when disturbed. The difference in behaviour between my study and Byrd and Allen's (2001) may be attributed to the limited number larvae that actually

survived to the second and third instar stages and were able to be identified as *P. regina* during my study. Since both *P. regina* and *L. sericata* had similar larval mortalities in the single species communities it is the addition of *C. rufifacies* that is detrimental to the survival and fitness of these individuals. Fitness as adults in the surviving individuals of *L. sericata* and *P. regina* is important because of the increase in larval mortality. *Phormia regina* adult fitness was dictated by community composition and in combination with the high larval mortality, over time in these conditions, *P. regina* would likely be excluded from the community. Although *L. sericata* was similarly affected by community composition and resource with respect to adult fitness, its larval mortality in the presence of *C. rufifacies* was as high compared to *P. regina* and therefore would likely persist in these communities.

Chrysomya rufifacies negative effects on these native blow fly species in nature maybe attributed to its role as an omnivore. Its mortality was not significantly affected by either resource type or species composition, however; its fitness decreased when it was the only species in the community. This was reflected in the decrease in adult size when *C. rufifacies* was in the single species communities. A study by Wells and Kurahashi (1997) showed that species that occur sympatrically with *C. rufifacies* are relatively resistant to its predation as compared to species not historically found together. This could give an advantage to *C. rufifacies* in its encounters with native blow fly species in the area. In Australia, *C. rufifacies* was shown to repel, compete and prey upon *L. sericata* and *L. cuprina* (Baumgartner 1993; Anderson *et al.* 1988; Tillyard and Seddon 1933). *Chrysomya rufifacies* may be limited in its expansion into southern Ontario due to

some physiological restraints such as a temperature flying threshold of 13ºC (Norris 1966; Vogt 1988). This result has already been observed as *C. rufifacies* larvae have only been recovered from carrion in the fall season, and are absent in the spring and early summer (Rosati and VanLaerhoven 2007) because of their lack of ability to overwinter at the typical temperature in this area (Norris 1966, Mackerras and Mackerras 1966, Greenberg 1971).

In addition to the importance of community composition, the basal carrion resource that the larvae feed upon is also important in their survival and fitness. As expected, all of the larvae that fed on the carrion resource of whole rat had the greatest fitness. Even though there were not marked differences between each of the resources in terms of what the nutritional analysis measured, there is clearly an advantage to the larvae if they feed on a variety of organs and tissues. This could be a result of different nutritional needs of certain minerals or amino acids found in different areas of the carrion which cannot be achieved through consuming only one type of tissue. Although there were differences among which of the individual tissue types produced larger adults, the results tended to relate to not only the resource type but also which community they belonged.

In my lab study, all of the communities were formed at the same time on each of the resources; however, in nature assembly does not always occur simultaneously and could attribute to greater success of these individuals. Holdaway (1930) and Fuller (1934) observed that each of the species within this feeding guild appeared to be using the resource in the same way, which is a counter example of Gause's competitive exclusion

principal (1934). However, when these communities were examined more closely, each of the species was actually exploiting the carrion in a different way (Denno and Cothran 1975) by seasonal, successional, and size gradients. The success of each of the species in my study on the whole rat could be attributed to some compartmentalization of the resource by each of the species. Because *P. regina* and *C. rufifacies* appear to utilize the resource in the same way by remaining on the resource until pupation and neither exhibiting extended wandering behaviour of *L. sericata*, *P. regina* could be an easier prey for *C. rufifacies* because it is readily available and in close contact with *C. rufifacies*. This resulted in high mortality and decreased fitness in *P. regina*. In nature, this may be avoided for much of their period of activity because in southern Ontario *C. rufifacies* is not present until the fall (Rosati and VanLaerhoven 2007), whereas *L. sericata* and *P. regina* are present together in the late spring, summer and early fall, with *P. regina* active earlier in the spring and later in the fall than *L. sericata* (Rosati and VanLaerhoven unpublished data) due to a lower developmental threshold allowing it to colonize into the cooler weather (Nabity *et al* 2006; Byrd and Butler 1997). Similar patterns of species' appearances throughout different seasons have been demonstrated in Southern California (Denno and Cothran 1975). *Lucilia sericata* and *P. regina* may be impacted at the end of the season by the presence of *C. rufifacies*; however the effects of that interaction should disappear before the next interaction the following fall. The coexistence of *L. sericata* and *P. regina* has been shown to occur due to how each of the species exploits the carcass as either the founder species with a preference for smaller carrion items, *L. sericata*, or the preference to exploit larger carrion, *P. regina* (Denno and Cothran 1975).

CONCLUSIONS

<u>Impacts on Communities</u>

The mechanisms of coexistence that occur within communities are still largely not understood. Many of the early studies of coexistence did not look at the mechanisms, but instead examined the compatibility with their environment (Arthur 1988) and comparing data set to models such as Lotka-Volterra. Competition among sympatric species is fairly common in nature although it is not universally found (Schoener 1983; Connell 1983). In ephemeral communities, such as carrion communities, species assemble together for only a few generations and then disperse. The regional species pool contributes to the species found in these communities and interactions that occur while these communities are assembled can cause shifts in species abundances based on the interactions that occur while the community is assembled. The dynamics of these communities can be changed by seasonal and successional patterns (Denno and Cothran 1975). The ability for these communities to sustain so many species on the same trophic level is due to resource partitioning and differences in niches. A study by Pianka (1974) demonstrated a correlation between the amounts of niche overlap in a lizard community to the amount of interspecific competition that occurred. Since a community with more niche overlap can support a great diversity of species this concept may help to explain the mechanisms of coexistence that are occurring within these communities.

Based on the results of my study, predation, competition, types of food resources and species composition all impact the mortality and fitness of blow flies and the occurrence of these species in nature. In my study, it was found that a potential overlap in

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niche between *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae) and *Phormia regina* (Meigen) (Diptera: Calliphoridae) could explain *P. regina* high mortality and resulting exclusion from communities containing both of these species. Both had the highest fitness when reared on the whole carrion, rat, and exhibited similar feeding behaviours. *Chrysomya rufifacies* success may be attributed to its ability to be a facultative predator during its later larval stages (James 1947; Hardy 1980; Shiao and Yeh 2008). Hutton and Wasti (1981) looked at *L. sericata* and *P. regina* during their larval development and determined that *P. regina* was a very weak competitor and in some cases was competitively excluded from a community by *L. sericata* when there were very high densities of individuals. However a study done in 2009 (Reid, unpublished data) showed that *L. sericata* could act as a facilitator species for *P. regina* under certain conditions and cause an increase in fitness for *P. regina*.

Some studies have shown that omnivory can stabilize food webs (Fagan 1997) despite what was originally found through theoretical literature suggesting that this would be destabilizing (Pimm and Lawton 1978). However the stability that omnivory can cause is based on the interaction strengths between the species when there are many weak interactions. The destabilizing effect can be seen when there is a very strong interaction between the species. My study found that the addition of *C. rufifacies*, which feeds on both the resource and the other species present, caused an extinction of one of the species, *P. regina*. This destabilization that occurred in this study may be a result of niche overlap in species that historically are not found in sympatry.

In nature, each of these species do not colonize typically at the same time and can be attracted to different types and sizes of carrion. *Lucilia sericata* is described as a pioneer species because it is usually, but not always, first to arrive at the resource followed by *P. regina* (Denno and Cothran 1975). *Chrysomya rufifacies* is usually classified as a secondary carrion fly (Fuller 1934a; James 1947; Mackerras and Fuller 1937) usually arriving after other species. Typically *L. sericata* prefers to exploit smaller carrion, but will also appear on larger resources (Smith and Wall 1997). On the other hand, *P. regina* and *C. rufifacies* both prefer larger resources. Again, with the behavioural similarities found in nature of *C. rufifacies* and *P. regina*, the results in this study confirm the potential seasonal displacement of *P. regina* by *C. rufifacies.* The behavioural differences between *L. sericata* and *C. rufifacies* in nature and in the lab experiment demonstrate the persistence of *L. sericata.* Hanski (1987) suggested that carrion communities have been saturated with species has lead to intense resource competition. This was studied with *C. rufifacies* and *Cochliomyia macellaria* (Fabricius) (Diptera: Calliphoridae) and results confirmed a displacement by *C. rufifacies* of the native species where they co-occur (Wells 1992; Wells and Greenburg 1992). My research also suggests this same species displacement event between *C. rufifacies* and *P. regina*.

As a response to competitive pressures the species in my study had a shift in their development time and stage durations when they were in a mixed community composition. Although geographically there are variations on developmental data (Gallagher *et al* 2010; Tarone and Foran 2006; Martinez-Sanchez *et al* 2007), differences were seen when comparing the single species data, which agreed with most of the

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literature, and the mixed species data, that did not fall into accepted ranges (Kamal 1958; Clark *et al* 2006; Byrd and Allen 2001). Development was faster in the mixed communities for all three species at different stages of development and the duration of some stages were also lengthened in response to the other species present. These changes in development time could be a result of competitive pressures, amount of resource available, or an increase in availability of some of the resource due to multiple species present and potentially breaking down the food resource differently.

My research brings to light a need for more knowledge in multispecies communities within the blow fly community. In terms of the application of this research, a lack of available data sets that take into account species interaction in their development could results in less accurate estimation of post mortem interval (PMI). Community ecology is essential to understand how these species interact within carrion communities and is causing a paradigm shift in forensic entomology from using single species data for time estimation to looking at factors beyond temperature data such as species interactions and the effect of the type of resource being consumed. Moreover, modification of interactions between different sets of species due to different basal resources has implications for various life history parameters including development rate, fitness and mortality of individuals. My research is not a comprehensive data set for such calculations, but it is a starting point for future work in this field.

Impacts of *Chrysomya rufifacies`* invasion has already been seen in the southern United Stated (Wells and Greenburg 1992), including the exclusion of native blow fly species on carrion items or the reduction of native individuals populations (Norris 1959),

and indications from my research suggest similar potential outcomes with two of the native species in Southern Ontario. Currently physiological constraints (Byrd and Butler 1997; Norris 1966; Vogt 1988) are preventing *C. rufifacies* from establishing permanently in this area, but adaptations and the effects of global climate change may result in the displacement of some of our native flies if permanent populations establish.

RECOMMENDATIONS

Future research and Applications

From the results of my research I would recommend that further study be done into multispecies carrion communities because my data show that these multispecies communities develop and behave differently from single species communities. This future research can contribute to the growing field of forensic entomology and the understanding of how species can coexist together on a single resource. I would also recommend further research into what components of a resource allow for increased fitness and survival of species in single and multi species communities. My data suggested that there are other benefits to individuals feeding on a single carrion resource (whole rat) than other resources (liver or muscle). A basic analysis was completed for a nutritional breakdown and the resources did not appear to differ based on these results. Investigation into what is causing a difference between the resources could contribute to the understanding of how multiple species are coexisting together. Lastly, I recommend as a result of my study, that the use of insects in forensic entomology should use multi species developmental data that reflect the environment that the larva developed in. Taking into account other species present and the interactions that cause developmental plasticity, changes in post mortem interval estimations could result more accurate estimations.

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