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ECOLOGY, BEHAVIOR AND BIONOMICS

Larval Distribution and Behavior of *Chrysomya rufifacies* (Macquart) (Diptera: Calliphoridae) Relative to Other Species on Florida Black Bear (Carnivora: Ursidae) Decomposing Carcasses

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Abstract
Larval interactions of dipteran species, blow flies in particular, were observed and documented daily over time and location on five black bear carcasses in Gainesville, FL, USA, from June 2002 – September 2004. *Cochliomyia macellaria* (Fabricius) or *Chrysomya megacephala* (Fabricius) larvae were collected first, after which *Chrysomya rufifacies* (Macquart) oviposited on the carcasses in multiple locations (i.e., neck, anus, and exposed flesh) not inhabited already by the other blow fly larvae. Within the first week of decomposition, *C. rufifacies* larvae grew to ≥12 mm, filling the carcasses with thousands of larvae and replacing the other calliphorid larvae either through successful food source competition or by predation. As a result, *C. macellaria* and *C. megacephala* were not collected past their third instar feeding stage. The blow fly species, *C. megacephala*, *C. macellaria*, *Lucilia caeruleiviridis* (Macquart), *Phormia regina* (Meigen), *Lucilia sericata* (Meigen), and *C. rufifacies*, completed two developmental cycles in the 88.5-kg carcass. This phenomenon might serve to complicate or prevent the calculation of an accurate postmortem interval.

Introduction

Chrysomya rufifacies (Macquart), the hairy maggot blow fly, was first recognized and named in 1843 by Macquart in the "Nouvelle-Hollande" region of Australia. It was found in Hawaii by the early 1900s, Japan in 1958 (Baumgartner 1993), and in other parts of the Asian and Australian Regions soon thereafter (Soos & Papp 1986). *Chrysomya rufifacies* was the first member of its genus to become established in the continental USA (Wells & Greenberg 1992a). It became established in several Southern border states between California and Florida, then moved north through the Midwestern states and south into the countries of Mexico, Guatemala, and Costa Rica (Baumgartner 1986, Byrd & Butler 1997, Mertins 1991, Steck & Butler 1991, Shahid *et al* 2000).

Chrysomya rufifacies is a necrophagous species with larvae that are. Facultative predators of larvae of other fly species (Fuller 1934, Williams & Richardson 1984, Baumgartner 1986, Early & Goff 1986, Goodbrod & Goff 1990, Wells & Greenberg 1992a, b, Shahid *et al* 2000). Since its arrival in the USA, *C. rufifacies* has used its predatory propensity to displace native blow fly species, such as *Cochliomyia macellaria* (Fabricius) (Baumgartner & Greenberg 1984, Goodbrod & Goff 1990, Wells & Greenberg 1992a, b, Byrd & Butler 1997, Wells & Sperling 1999, del Bianco Faria *et al* 1999, Shahid *et al* 2000).

Invertebrates that feed on carrion appear at a carcass in transitioning patterns of succession that can be directly associated with stages of carcass decay. The first generation of initial colonizers provides a biological clock that can be used to estimate the time of insect arrival and approximate the time of death. Flies in the family Calliphoridae are the most common carrion colonizers both in diversity and abundance (Goddard & Lago 1985). Some researchers stated succession as a method for predicting time sequences because the adults of certain calliphorid species were believed to visit

carcasses only during specific stages of decomposition (Goddard & Lago 1985).

The objectives of this study were to observe and document the temporal and spatial distribution and behavior of *C. rufifacies* larvae relative to other calliphorid species on decomposing Florida black bear, *Ursus americanus floridanus* carcasses. We hypothesize that the introduced species *C. rufifacies* will out-compete the native blow fly species because of their predatory behavior, resulting in altered successional patterns among native species.

Material and Methods

The study was conducted in a 15.24×9.14 m fenced area on semi-wooded land at the Florida Fish and Wildlife Conservation Center (FFWCC) in Gainesville, FL (29°39′7.19″ N, 82°19′29.97″ W). The five bear carcasses used in this study (Table 1) were from bears which were killed by cars at locations within a 2-h drive from Gainesville, FL (near the Ocala National Forest). Carcasses were transported to the FFWCC by a Florida Fish and Wildlife officer within 24 h. The carcasses were received one at a time throughout the study months as these deaths occurred. Bear carcasses were used because there is sufficient flesh for the complete development of maggot masses similar in size to those collected from human remains. Carcasses were not placed in protective structures to exclude vertebrate scavengers; however, scavenging never occurred. Bear carcasses were not moved following placement at the FFWCC. As soon as possible to their arrival, each bear was visited and documentation was made of time, any visible wounds or trauma, insect activity, and dipteran egg masses. Bear weights and sampling periods ranged from 17.2 to 117.9 kg and 7 to 21 days, respectively (Table 1).

To document temporal distribution of larvae on all five bear carcasses, collections were made daily at approximately 1630–1800 hours until active carcass decomposition was completed (cessation of larval dispersal). After active decomposition was complete (1- to 2-week postmortem), collections were made every three days until insect activity ceased. Before the daily samples were collected, observations were made of each bear to document the spatial distribution of larvae in general and the larval relationships after *C. rufifacies* were present.

Larvae were collected during each visit from the maggot masses typically located at the head, abdomen and anus of the carcass. During the first 48 h after carcass arrival, eggs and 1st- and 2nd-instars were collected with a forceps (≥150 larvae/collection container) and retained separately by their location on the carcass. After 48 h, all species of larvae were collected from the largest maggot masses (≥10 cm) located typically at the head, abdomen and anus of the carcass by removing three full tablespoons (~15 mL each) or three gloved-finger-tip grabs of larvae. Live larvae were placed in empty collection containers. *C. rufifacies* larvae could be identified in the field based on their hairy appearance with a transverse row of fleshy tubercles medially on each segment, however the identifications of all collected larvae were confirmed in the laboratory. Larvae collected prior to the late third instar wandering phase were boiled in water for approximately 10 sec to fix internal proteins and prevent further decomposition, then placed into vials of 70% ethanol for preservation. Third instars were identified to species using the keys of Stojanovich *et al* (1962) and Wells *et al* (1999). Late third instars in the wandering phase were reared to adults in an environmental chamber (26.7°C and 60% RH) to confirm identification of adults collected by sweep net.

At each visit during active decomposition, adult flies were collected with a sweep net that was waved over the carcass 5–7 times. Captured adult flies were killed in ethyl acetate and identified to species if possible (James 1947, Smith 1986, Catts & Haskell 1990). Daily ambient temperatures were recorded in the study area with a HOBO™ external logger (Onset Computer Corporation, Bourne, MA, 1995–1999) throughout decomposition.

Statistical analysis was done with SAS 9.2 (2002). Student–Newman–Keuls test was conducted.

Table 1 Bear weight, sex, estimated time of death, final date, and mean ambient temperature for decomposition period.

Bear number	Weight (kg)	Sex	Date and time of death (est.)	Initial visit date and time	Final visit date	Mean ambient temperature±SE
1	75.6	F	2 June 2002 Evening	3 June 2002 1645 hours	23 June 2002	25.02°C±0.28
2	88.5	F	30 Aug 2002 0800 hours	30 Aug 2002 1910 hours	26 Sep 2002	25.26°C±0.12
3	17.2	M	1 Nov 2002 ±0000 hours	1 Nov 2002 1330 hours	13 Nov 2002	19.91°C±1.56
4	40.8	M	1 July 2004 ±1200 hours	2 July 2004 Hours unknown	13 July 2004	25.30°C±0.53
5	117.9	M	15 Sep 2004 ±0000 hours	16 Sep 2004 1300 hours	4 Oct 2004	24.25°C±0.29

Results

The daily mean ambient temperatures ranged between 13°C and 34°C during the study period with overall mean ambient temperature±SE for the periods varying just slightly and presented in Table 1. The highest and lowest ambient temperatures recorded for the June 2002 bear carcass were 27.3°C and 23.3°C, respectively. In September 2002, the maximum temperature, recorded 3 days postmortem was 26.1°C, and the minimum temperature, which occurred 11 days later, was just 24.1°C. On 1 November 2002, the highest ambient temperature recorded was 34.1°C and the lowest mean ambient temperature for this study, recorded on 13 November 2002, was 11.8°C.

The following six species of adult and immature calliphorid flies were collected from the bear carcasses: *C. rufifacies, C. megacephala* (Fabricius)*, C. macellaria, Lucilia caeruleiviridis* (Macquart)*, Phormia regina* (Meigen), and *Lucilia sericata* (Meigen). Eggs were observed on all carcasses within 24 h, followed by 1st and 2nd instars at 24 and 48 h, respectively (Fig 1). The oldest of these larvae were molting into the 3rd instar at 72 h and were more readily identified using larvae keys (Stojanovich *et al* 1962, Wells *et al* 1999) (Table 2). The distinct morphological features of *C. rufifacies* made possible the identification in the 1st and 2nd instars. By day 7, *C. rufifacies* became the dominant species and inhabited all areas of the carcasses until soft tissue was no longer available (ca. 12 days).

In one instance, on bear 2, on day 12 after all *C. rufifacies* had pupated, eggs were observed and a second group of blow flies lacking distinctive *C. rufifacies* features began their development. However by day 22, *C. rufifacies* was once again the only blow fly species on the carcass (Fig 1).

A key behavioral characteristic was the later appearance of *C. rufifacies* larvae in the carcasses despite the constant presence from day 1 of adult *C. rufifacies* which were observed resting in the trees surrounding the carcasses. For all of the carcasses, *C. rufifacies* adults were not collected via sweep net until 24 h postmortem or later. In four of the five bear carcasses, *C. rufifacies* larvae were collected one day after the collection of the other identifiable blow fly larvae (*C. megacephala, C. macellaria, L. caeruleiviridis, L. sericata,* and *P. regina*) (Table 2).

Chrysomya rufifacies oviposited at the ground-carcass interface, at sites where other blow fly larvae were not present. Egg masses where seen throughout the fur of the carcass not in correlation with the orifices. The other calliphorid species oviposited in carcass orifices or wounds. As *C. rufifacies* larvae matured into the third instar, they began to occupy larger areas of the carcass and displace the other blow fly larvae (Table 2).

There were a few notable variations in larval species composition from the five different bears. In June 2002, *Fannia canicularis* L. was collected and in August 2002, *Wohlfahrtia* sp. was collected, but not at any other time. The species

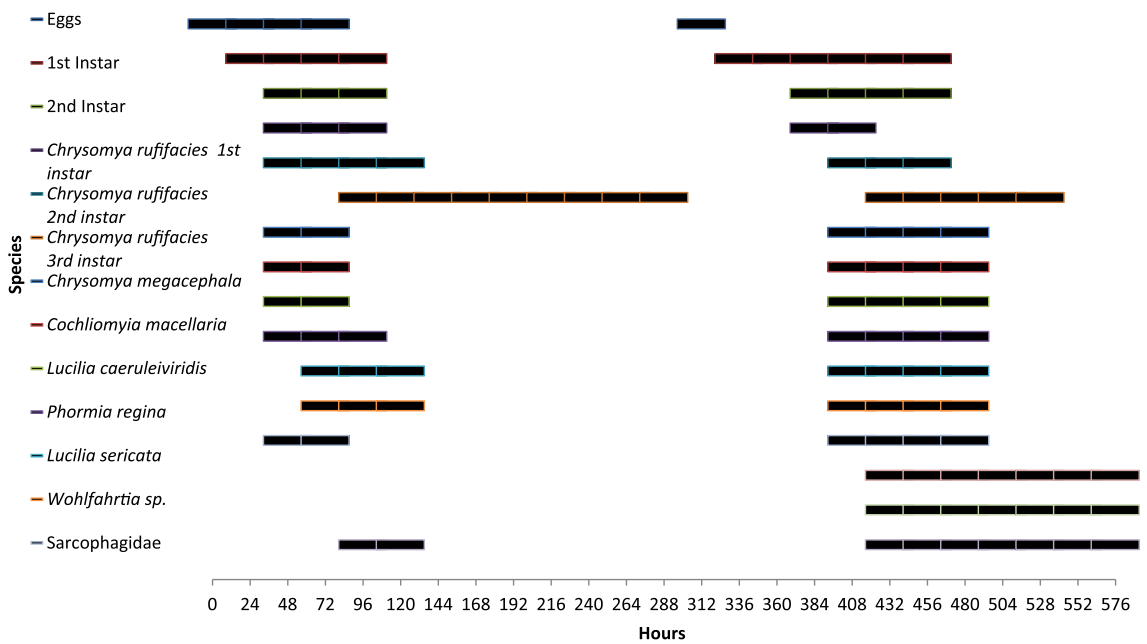

Fig 1 Larval succession pattern during decomposition for bear 2, August 2002; data show the arrival and departure for each life stage and species from the bear carcass.

Table 2 Daily postmortem collection means of developing blow fly larvae from bear carcasses.

	24	48	72	96	120	144	168	192	216	240	264	288	312	384	456
Eggs	117±98.69	284±147.42	37±20.01			3±3							5±4.8		276±275.8
1st instars		75±58.1	391±364.65	28±16.88									47±47	44±44	
2nd instars			217±161.63	21±14.18	0.2±0.2	0.4±0.4								54±54	
1st *Chrysomya rufifacies*				9±8.67											
2nd *Chrysomya rufifacies*			120±118.42	464±268.08	81±80.05	1±0.58				0.5±0.5		0.25±0.25		0.5±0.5	0.5±0.5
3rd Chrysomya *rufifacies*			0.2±0.2	428±230.17	332±191.09	184±122.87	181±107.98	162±93.87	57±40.89	135±135	8±7.8	50±40.54			
Chrysomya megacephala			82±74.26	67±56.97	0.25±0.25	2±2.25								14±14	0.5±0.5
Cochliomyia macellaria			42±27.42	6±4.76	6±4.86									19±18.5	0.5±0.5
Lucilia caeruleiviridis			22±15.09	53±37.76	0.25±0.25									1±1	0.75±0.75
Phormia regina			23±21.5	16±14.5										0.67±0.67	0.67±0.67
Lucilia sericata			0.67±0.67	10±8.69	2±2.33									0.33±0.33	11±11

Data represent all larvae collected hours postmortem for each of the five bear carcasses used in this study. Eggs and 1st and 2nd instars (which were not *Chrysomya rufifacies*) were not identified.

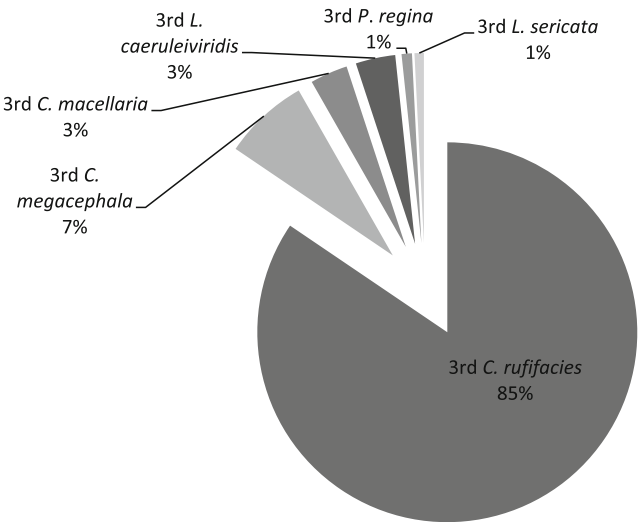

Fig 2 Percentage comparison of blow fly larvae collected throughout decomposition of black bear carcasses depicting *Chrysomya rufifacies* as the dominant species in North Central Florida.

composition in November 2002 was limited to the five calliphorid species commonly found in North Central Florida: *C. rufifacies, C. megacephala, C. macellaria, L. caeruleiviridis*, and *L. sericata*. The larvae from bears during June 2002 and September 2004 were limited to just four different dipteran species. The third bear, a cub weighing 17.2 kg (Table 1), decomposed completely within 144 h, compared with the other bears that required 480, 648, 240, and 336 h, respectively.

When the percentages of each larval species collected throughout decomposition are presented graphically, it becomes obvious that *C. rufifacies* was the dominant species present on the carcasses during the decomposition process (Fig 2). *Chrysomya rufifacies* larvae were significantly more abundant ($p < 0.0001$) in comparison with all other larval fly species throughout decomposition period for all five bear carcasses. Species collection and composition for bears 1, 2, and 3 were found to be significantly different than bears 2 and 5 (Table 3).

Discussion

Larvae of six forensically significant calliphorid species were found on the bear carcasses. However, after *C. rufifacies*

Table 3 Species collection and composition comparison for all bear carcasses with Student–Newman–Keuls Test.

Species mean collection	Bear	Grouping
94.32	3	A
90.80	1	A
83.78	2	A
11.23	4	B
3.91	5	B

reached the third instar, the five other calliphorid species (*C. megacephala, C. macellaria, L. caeruleiviridis, P. regina,* and *L. sericata*) rapidly disappeared. The study sites did not contain puparia from blow fly species other than *C. rufifacies.* Survivorship of the native species is not completely known but data show a significant and sudden decrease in population due to the presence of *C. rufifacies.* These calliphorids constitute a comparatively narrow species diversity compared with other regions of the USA where numerous dipteran species are present on decomposing corpses and their relationships and developmental times have been well documented (Goddard & Lago 1985, Goff 1991, 1993, Byrd & Butler 1996, 1997, 1998). The mean ambient temperature range recorded during the decomposition of all five bear carcass, i.e., from 25.3°C in late summer to 19.9°C in the fall, showed little variation and should not have impacted the species of Diptera present.

Gruner *et al* (2007) recovered seven calliphorid species from pig carcasses in Florida, but this might differ due to the larger size of the bear carcasses. Davies (1999) noted that some blow fly species have a carcass size preferential and are rarely found on carcasses that are not within their desired size range.

Phormia regina was not collected during the month of November in our study or by Gruner *et al* (2007); however in contrast to Gruner *et al* (2007), *C. megacephala* was collected from all the bear carcasses during our study.

With the exception of *C. rufifacies*, the 1st and 2nd instar calliphorid larvae collected during our study (Table 2) have similar taxonomic characteristics which prevent their identification to species until the 3rd instar (Stojanovich *et al* 1962, Wells *et al* 1999). Behaviorally the species were similar in that larvae grew quickly and formed maggot masses of 2.5–10 cm wide. When these species were late 2nd and early 3rd instars, *C. rufifacies* larvae were in the 1st and 2nd instars and located on the side of the carcass opposite to that of the other larval species. This phenomenon was also observed by Goodbrod & Goff (1990) in laboratory studies.

Upon molting into the third instar, *C. rufifacies* larvae moved throughout the carcass and either consumed the larvae of the other fly species or forced them to leave the carcass. Premature dispersal could lead to higher larval mortality with a concomitant reduction in pupae. Larvae of species other than *C. rufifacies* were never observed dispersing from a carcass nor were pupae of any species other than *C. rufifacies* found near the carcasses. Therefore, it would seem possible that the missing larvae may have been consumed by the 3rd instars of *C. rufifacies.* Although this was not confirmed with diagnostic techniques, the cannibalistic behavior of *C. rufifacies* has been observed previously under laboratory settings (Wells & Greenberg 1992a) when *C. macellaria* and *C. rufifacies* were reared together.

This phenomenon is not unexpected and has been predicted by other researchers (Baumgartner 1993, Goff 2000). This behavior alters the species composition found on a carcass because some species are easier prey for *C. rufifacies* than others (Wells & Greenberg 1992a). Depending upon the degree of species alteration that has occurred when a carcass is found, it could prove difficult to compare postmortem interval (PMI) data from northern regions of the USA with those from Florida, Hawaii and other states located in the southern US. When comparing the effects of the introduction of *C. megacephala* on *C. macellaria*, it was noted that the spatial dimension stabilized itself and had little effect on the population (Godoy *et al* 1997). That does not appear to be the case when *C. rufifacies* is introduced into a new location, because the native species are no longer collected in large numbers.

An interesting phenomenon was observed only with the second bear carcass. After the first-wave (Smith 1986) of *C. rufifacies* larvae had pupated, the carcass was considered devoid of blow fly larvae. However, 48 h later, a second wave of flies invaded the remains (Fig 1). If the first larval collections had been made on this carcass >456 h (19 days) after the death of the bear by an inexperienced individual and pupae were not collected from the scene, the PMI may have been miscalculated. Larvae collected at 456 h were 3rd instars. When larval samples shipped to an entomologist for PMI calculation without accompanying decomposition pictures are referenced to the ambient temperature, a PMI, incorrect by a few days would be calculated instead of the 19-day PMI.

Data suggest the formation of a second wave of dipteran activity in Bear 1 which no longer exhibited visible soft tissue, but fly development ceased before this could be verified. The occurrence of late oviposition by adult blow flies was reported by Shean *et al* (1993), but data showing complete development to the adult stage were not presented.

The most abundant blow fly species collected on the bear carcasses during this study was the hairy maggot blow fly, *C. rufifacies* (Fig 2). The senior author (S.L.S.) observed that the hairy maggot blow fly is one of the earliest to arrive at a carcass but the adults wait several hours before ovipositing. This delay allows the eggs of other dipteran species already present in the carcass to hatch into 1st instar larvae before the *C. rufifacies* hatch from their eggs and begin development. To our knowledge, this is the first time this behavior has been observed in the field. However, it has been noted in Hawaii that *C. rufifacies* will hesitate to oviposit in the absence of *C. megacephala* eggs or early instar larvae under laboratory conditions (Goff *et al* 1988).

The current study provides field documentation about the invasive and predatory behavior of *C. rufifacies.* This behavior coincides with observations made by Wells & Greenberg (1992a) but it has not been observed or reported in Florida. This information is important to forensic entomologists working in the Southern US, especially in Florida, where

one could falsely assume that *C. rufifacies* was the only fly able to locate a corpse or carcass because it was the only fly species present. This would not be true in the case of *C. rufifacies* because they utilize the larvae of other fly species to complete their development (Fuller 1934, Goodbrod & Goff 1990, Shalaby *et al* 2000).

Another important factor is that *C. rufifacies* has made its way throughout the USA, displacing the native calliphorid species and becoming the dominant fly on decomposing remains (Gagne 1981, Baumgartner 1986, Martin *et al* 1996, Byrd & Butler 1997, Shahid *et al* 2000). Thus, the larvae of native fly species may be selected for those having shorter development cycles which are needed to prevent their displacement and consumption by the larvae of *C. rufifacies.*

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