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Resource use by an introduced and native carrion flies

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Abstract The carrion fly *Chrysomya rufifacies* has recently been introduced to North America. Larvae of this species are facultative predators on other carrion larvae, and are known to reduce populations of the New World fly *Cochliomyia macellaria* in the laboratory and in certain field situations. In order to identify conditions under which native taxa might avoid interaction with the invader, we examined broad patterns of resource use by capturing postfeeding larvae as they left a carcass. The Calliphorinae were least similar to *C. rufifacies* since they were able to exploit smaller carrion, showed a peak in density during cold weather while *C. rufifacies* numbers were low, and occurred much earlier than the invader during succession within a carcass. *Phormia regina* also was most abundant during cold weather. The Sarcophagidae were able to exploit smaller carcasses than the invader but are likely to encounter it in larger carcasses. *C. macellaria* was the species most similar to *C. rufifacies* in carrion use, and probably is reduced in number by the invader wherever they coexist. In contrast to all other taxa, *C. rufifacies* exited a carcass alone, suggesting that other larvae of the same age were attacked. Manipulation of a conspicuous predator, the ant *Solenopsis invicta,* revealed a negative effect on numbers of *P. regina* and *C. macellaria.*

Key words Calliphoridae · Sarcophagidae · Biological invasion · Resource partitioning · *Solenopsis invicta* predation

Introduction

Biological invasions have attracted a great deal of attention because of the ecological and economic harm they may cause (Elton 1958; Crosby 1986; Mooney and Drake 1989; Simberloff 1991). Efforts to slow the widespread disruption of native ecosystems are hampered by our inability to evaluate the probability of success and ecological impact of a potential invader (Lodge 1993). Hypotheses concerning those properties that make a species more likely to invade are difficult to test because, with the exception of biological control efforts, deliberate introductions would be impractical. Even a posteriori conclusions concerning the impact of an invader on native species are seldom based on careful investigations (Simberloff 1991), although these may be the experiments most available to those interested in invasion ecology. This study is part of an ongoing effort to measure the effects of invaders that appear to be displacing a native species, and in which the taxa concerned are amenable to experimental manipulation.

Recently the Western Hemisphere has been invaded by four Old World blow flies (Calliphoridae) in the genus *Chrysomya. C. albiceps, C. putoria,* and *C. megacephala* appear to have accompanied Angolan refugees to Brazil in 1975–1976 (Guimarães et al. 1978, 1979). Since that time they have spread rapidly across South America (Mariluis 1981; Baumgartner and Greenberg 1984; Baumgartner 1988), and *C. megacephala* has become established in the Los Angeles area (Olsen and Sidebottom 1990; Wells 1991). A fourth species, *C. rufifacies,* was collected in Costa Rica in 1978 (Jirón 1979), and was the first of the *Chrysomya* species to reach North America (Gagné et al. 1982). It can now be found throughout the southwestern USA (Richard and Ahrens 1983; Baumgartner 1986; Greenberg 1988) and in Miami, Florida (Baumgartner 1993).

The natural history of carrion flies (Calliphoridae and Sarcophagidae) is thought to include severe competition for larval food. Almost every aspect of their breeding biology suggests intense selection for rapid location and

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consumption of this patchy and ephemeral resource (Beaver 1984; Hanski 1987). A carcass often receives more eggs or larvae than the food can support (Holdaway 1930; Salt 1932; Fuller 1934; Kneidel 1984), and the resource is typically consumed within one generation of the arthropods (Beaver 1984). The experimental exclusion of some species from carrion has resulted in an increase in competitor populations (Denno and Cothran 1976; Wells and Greenberg 1992b), and even the appearance of species not otherwise seen (Kneidel 1984).

In previous experiments, we found that *C. rufifacies* reduced the number of *Cochliomya macellaria* bred from rabbit carcasses in the field (Wells and Greenberg 1992b) and that a highly asymmetric competition occurred between larvae of the two species in the laboratory (Wells and Greenberg 1992c). The competitive superiority of *C. rufifacies* undoubtedly results from its facultative predation on other larvae. In laboratory petri dishes almost all attacks by *C. rufifacies* on *Co. macellaria* occurred between individuals in the third (final) stadium (Wells and Greenberg 1992a).

Coexistence between carrion flies is often facilitated by partitioning of the carrion resource according to season (Denno and Cothran 1975; Hanski and Kuusela 1980; Meskin 1986), carcass type (often interpreted as the effect of size) (Mönnig and Cilliers 1944; Schoenly and Reid 1983; Kneidel 1984), habitat (Macleod and Donnelly 1957; Hanski 1976; Early and Goff 1986) and succession within a single carcass (Schoenly and Reid 1987). It was, therefore, possible that *C. rufifacies* and *Co. macellaria* generally avoid the competition we observed under relatively restricted conditions.

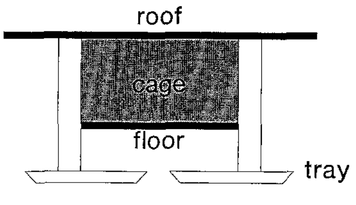
In this study we examined patterns of food use by larvae of *C. rufifacies* and native carrion flies at a site in Texas, United States. We focused on those axes of the food resource commonly partitioned by carrion flies in an effort to find ways that native taxa might avoid competition with the invader. Because the most conspicuous predator of fly larvae, the red imported fire ant, *Solenopsis invicta,* could be easily manipulated within our design, its effect was measured in an attempt to detect predator-mediated coexistence (Paine 1974).

Materials and methods

Experimental design

During September 1989 to July 1990, freshly thawed carcasses that had been frozen immediately following death were exposed to arthropod activity at several locations in Kerr and Gillespie Counties, Texas (Wells 1992). Each carcass was used to bait a trap (Fig. 1) which excluded scavenging vertebrates. Each rat-baited trap was placed within a second metal cage since their small size made them vulnerable to disturbance. Pans filled with kerosene were arranged around each cage to trap and preserve postfeeding larvae, which crawl away from the body; they were collected each day. The legs of each trap were in the kerosene and so crawling arthropods were excluded. Preliminary observations revealed no repellent effect from the presence of kerosene.

The design was that of a balanced, multi-factorial experiment with the following experimental factors: (1) carcass type (200–300 g albino laboratory rats killed by decapitation, 1–2.5 kg domestic rabbits killed by a blow to the head, and 7–12 kg Angora goats killed by a blow to the head); (2) habitat (urban, rural pasture, and rural woods); (3) presence versus absence of *S. invicta* (access to each carcass was permitted by bridging the kerosene with several sticks, which the ants readily crossed when they were active); and (4) sampling period (=season). No arthropods other than fire ants were observed to cross the sticks onto a carcass.



Dimensions (m)	rat	rabbit	goat
roof area	.36 X .51	1 X 1	1 X 1.3
floor area	.13 X .2	.43 X .43	.43 X .76
cage height	.1	.25	.3

Fig. 1 Design of traps used to collect postfeeding larvae

During a sampling period, then, two rats (with and without ants), two rabbits and two goats were simultaneously exposed at sites in three habitats, and left in place until maggot activity had apparently ceased. Traps at each site were arranged equidistant from each other on a circle 40 m in diameter with a randomly determined compass orientation. Trap location and the assignment of carcasses to traps were randomized within each sampling period. Sites from each habitat were chosen at random from at least two new possibilities each sampling period.

Larvae were separated by instar, and third instars identified, where possible, to species using the keys of Hall (1948), Furman and Catts (1982), Skidmore (1985) and Liu and Greenberg (1989). Calliphorinae were not separated to species for logistical reasons and no good keys were available for Sarcophagidae. A lower size limit of half the observed maximum was used to choose larvae likely to have completed development since this is approximately the minimum recorded for several calliphorid species (Levot et al. 1979). This choice was rarely made except for specimens of *C. rufifacies*, which were often sampled when the food had been nearly consumed (see Results). Although efforts were made to examine many of the smaller larvae, it was not possible to screen them all. As a result it may be that small species such as Sepsidae, Piophilidae or Phoridae were discarded along with the undersized calliphorids. Adult flies within the study area were regularly observed and collected (either as adults or reared from larvae) on other carrion during the experiment in order to note those that might be present as larvae. An unknown number of larvae escaped capture by falling between the pans (except in traps baited with rats which were entirely within one pan), but our observations suggested that each species had an equal probability of being captured.

C. rufifacies may pupariate beneath the carcass itself (Fuller 1934). Preliminary observations indicated that this occurred with the goat carcasses used, and began around the edge as that portion of the carcass became dry. In order to monitor this behavior during the experiment, the edge of a carcass was lifted slightly each day for observation once *C. rufifacies* larvae appeared in the samples. Very few *C. rufifacies* puparia were discovered under the rabbit carcasses and the species was not bred from rats (see Results).

Statistical analysis and summarization

The total number of larvae of each taxon from each carcass was transformed to $\ln(Y+1)$, and subjected to a separate analysis of variance (ANOVA) (SAS Institute 1985). Season, carcass type, ants (+, –) and habitat were the main effects. The large number of zero values (taxon absent from a carcass) made the full data set inappropriate for ANOVA. Because *C. rufifacies* was not collected from rats, rat carcasses and the rare flies (all the Muscidae) were not included in the analysis. The degree to which different taxa appeared together in daily samples was quantified using an index of proportional overlap $C_{ih}=1-1/2\Sigma|p_{ij}-p_{hj}|$ where p_{ij} and p_{hj} are the proportion of the larvae of taxa *i* and *h* from a carcass that were collected on day *j* (Colwell and Futuyma 1971). This index was developed to measure niche overlap, but our purpose was to summarize striking differences observed in the mixing of species in our samples. C_{ih} varies from a values of 1 (complete proportional overlap) to 0 (no overlap).

Results and discussion

All higher Diptera collected at carrion either during these experiments or from other carrion within the study area are listed in Table 1. Species known to have actually bred in carrion were collected as larvae and identified in that stage or reared to adults. This was the first record of *C. megacephala* in the contiguous United States outside southern California (Wells 1991).

More than 220,000 postfeeding larvae were judged large enough to have completed development. The taxa identified in samples from the experiment are given in Table 2, which shows the occurrence of these larvae in different carcass types.

The Calliphorinae and Sarcophagidae, although not separated to species, form genuine carrion guilds (Denno and Cothran 1975, 1976) and so are useful ecological entities. The species were likely to be the same as the adults observed on carrion during the study. Of the Calliphorinae, these were *Phaenicia mexicana* and to a lessor extent (approximately 10% of sweep samples) *P. sericata* during warm weather, and *Cynomyopsis cadaverina* along with only a few specimens of *Calliphora coloradensis* during cold weather. The large size of the Sarcophagidae in our samples suggested that most were either *Sarcophaga bullata* or *S. sarracenioides.*

The increase in number of taxa per carcass as carcass size was increased (Table 2), appeared to result from the addition of species that typically arrive later. The low number of carcasses yielding *P. regina* reflects the seasonality of this cold-weather fly (Fig. 2).

It was found that *C. rufifacies* in goat carcasses began to pupariate beneath the carcass itself about midway through the period in which this species appeared in the samples. Typically a carcass had become rather dry by this time and perhaps more suitable for pupariation for that reason. Rough estimates made by volume indicated that about 30% of the total *C. rufifacies* from each carcass remained in this manner. For this reason *C. rufifacies* sample totals were an under count relative to the other species, and the mean time from exposure to the collection of postfeeding larvae is an underestimate of the true mean. Our failure to discriminate among species of Calliphorinae or Sarcophagidae made this a poor test of seasonality in these groups, since we could not detect the seasonal replacement of species that commonly occurs (Denno and Cothran 1975; Kentner and Streit 1990

Table 1 Diptera collected either as larvae or adults in Kerr and Gillespie Counties Texas. A *question mark* indicates a species that could have been included in samples that were not separated to the species level

	Adults	Larvae
CALLIPHORIDAE		
Phaenicia sericata (Meigen)	+	+
P. mexicana (Macquart)	+	+
Calliphora coloradensis Hough	+	?
Cynomyopsis cadaverina (Robineau-Desvoidy)	+	?
Phormia regina (Meigen)	+	+
Cochliomyia macellaria (Fabricius)	+	+
Chrysomya rufifacies (Macquart)	+	+
C. megacephala (Fabricius)	+	–
SARCOPHAGIDAE		
Sarcophaga bullata Parker	+	+
S. sarracenioides Aldrich	+	+
Oxysarcodexia ochripyga (Wulp)	+	?
O. ventricosa (Wulp)	+	?
Ravinia derelicta (Walker)	+	?
Ravinia sp. near *ochracea* (Aldrich)	+	?
Blaesoxipha plinthopyga (Wiedemann)	–	+
MUSCIDAE		
Muscina stabulans (Fallén)	–	+
Synthesiomyia nudiseta (Wulp)	+	+
Neomusca tripunctata (Wulp)	+	–
Musca domestica Linnaeus	+	–
Ophyra aenescens (Wiedemann)	+	+
O. ignava (Harris)	–	+
Hydrotea dentipes (Fabricius)	–	+
PHORIDAE		
Megaselia scalaris Loew	+	–

Table 2 Number of carcasses out of 24 from which each taxon of larva was collected, and in parentheses the mean number of larvae collected per occupied carcass

	Rat	Rabbit	Goat
Calliphorinae	15(357)	23(3010)	24(2666)
Sarcophagidae	16(62)	20(70)	21(89)
Cochliomya macellaria	1(91)	14(454)	23(1648)[a]
Chrysomya rufifacies	0	21(580)	24(880)
Phormia regina	0	9(348)	10(360)
Hydrotea dentipes	0	1(6)	5(108)
Fannia scalaris	0	1(1)	8(22)
Synthesiomyia nudiseta	0	0	1(4)
Ophyra aenescens	0	0	1(12)
O. ignava	0	0	1(1)

[a] Large numbers pupariated in carcass (see text)

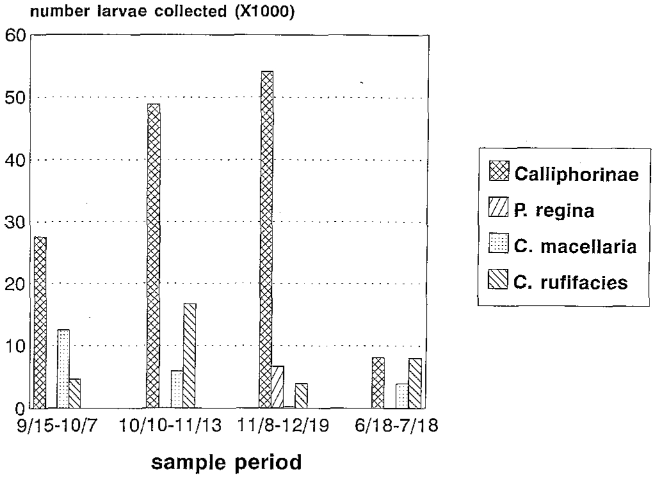


Fig. 2 Total number of each taxon collected according to sample period

and unpublished). It may also be that this sampling technique resulted in an undercount of the muscid species since they have been known to flourish in dried carcasses that were subsequently wetted by rain (T. Tantawi 1991, personal communication), and all carcasses in this study were sheltered.

Sample totals

Significant results of each ANOVA are shown in Table 3. We believed that a native taxon might avoid the invader if it were relatively abundant in situations where *C. rufifacies* was relatively rare. The following differences were found in the patterns of *C. rufifacies* versus the native taxa.

Carcass type

C. rufifacies was never collected from rat carcasses, while Calliphorinae and Sarcophagidae regularly were (Table 2). Goat carcasses produced significantly more *C. macellaria,* but it is likely that we missed a similar effect for *C. rufifacies* (Table 2).

Season

The mean air temperatures recorded during each sampling period are given in Table 4. During the coldest period of the study, *C. rufifacies* and *Co. macellaria* were relatively scarce, while *P. regina* and the Calliphorinae were relatively abundant (Fig. 2).

Succession

The rank of each taxon within each sampling period (Table 4) suggests that the Calliphorinae are regularly the first, and *C. rufifacies* regularly the last, of these common forms to appear as postfeeding larvae, while the others are more variable in position. Since the values for *C. rufifacies* recorded here are certainly underestimates (see above), it is even more likely to be the last of these taxa to leave a carcass.

The degree to which the different taxa overlapped in samples can be seen in Table 5. Compared to all the other taxa considered, *C. rufifacies* exited these carcasses unaccompanied by other species. Again, since our sampling was biased toward earlier *C. rufifacies*, the overlap with the natives was actually even less. This pattern could reflect differences in arrival and development times, but given *C. rufifacies,* unique predaceous habits, a likely explanation is that other species of the same stage had been consumed by the invader.

Summary of evidence for resource partitioning

The Calliphorinae, by virtue of their use of the smallest carcasses, greatest abundance in winter, and earliest position in succession, appeared to be the native taxon least likely to interact directly with the invader. Further investigation of individual calliphorine species, particularly those that are abundant in warm weather, may find exceptions to this pattern. *P. regina* may also avoid *C. rufifacies* according to season, as did those Sarcophagidae that bred in rats. *Co. macellaria* did precede *C. rufifacies* in succession, but the absence of *Co. macellaria* during the following "wave" of *C. rufifacies* suggests that this may be because later individuals were attacked. In addi-

Table 3 Summary of ANOVA results for carcass totals of each taxon

Taxon	Experimental factor	df[a]	F	Prob.>F
Calliphorinae	Season	3/23	7.03	0.002
	Ants (+,–)	1/23	0.91	ns
	Habitat	2/23	2.04	ns
	Carcass type	1/23	0.00	ns
Sarcophagidae	Season		2.19	ns
	Ants (+,–)		0.19	ns
	Habitat		4.33	0.03
	Carcass type		0.04	ns
P. regina	Season		77.76	0.0001
	Ants (+,–)		4.28	0.05
	Habitat		1.62	ns
	Carcass type		2.1	ns
Co. macellaria	Season		10.32	0.0002
	Ants (+,–)		9.6	0.005
	Habitat		4.72	0.02
	Carcass type		49.7	0.0001
C. rufifacies	Season		5.43	0.006
	Ants (+,–)		0.01	ns
	Habitat		2.59	ns
	Carcass type		2.28	ns

[a] Other taxa follow pattern of Calliphorinae

Table 4 **A** Mean number of days from exposure of rabbit and goat carcasses to the appearance of postfeeding larvae in samples for each sampling period. The ranks of the more common taxa are given in parentheses. **B** Mean of daily high and low air temperatures (°C) Recorded by USDA in Kerrville, Texas during the experiment

	9/15–10/7	10/10–11/13	11/8–12/19	6/18–7/18
A				
Calliphorinae	7.18 (1)	6.05 (2)	9.75 (1)	4.12 (1)
Sarcophagidae	10.26 (3)	5.19 (1)	13.16 (2)	4.38 (3)
Phormia regina	6.21[a]	5.36[a]	15.75 (4)	6.00[a]
Cochliomya macellaria	7.32 (2)	8.01 (3)	13.62 (3)	4.09 (2)
Chrysomya rufifacies	11.42 (4)	10.56 (4)	20.40 (5)	5.96 (4)
Hydrotea dentipes	22.00	–	14.90	–
Fannia scalaris	22.00	17.78	21.51	6.00
Synthesiomyia nudiseta	7.50	–	–	–
Ophyra spp.	22.00	–	–	12.00
B				
mean air temperature during period	20.0	16.1	9.2	28.1

[a] only 1% of *P. regina* collected during these periods

tion, while *C. rufifacies* numbers were not affected by *S. invicta,* the ant did reduce *Co. macellaria* and *P. regina,* and if anything should aid the invader. We found no evidence that the reduction in *Co. macellaria* numbers caused by *C. rufifacies* in the laboratory (Wells and Greenberg 1992c) and in rabbit carcasses during summer in the field (Wells and Greenberg 1992b) does not occur widely within the study area.

The Sarcophagidae could occur even later than *Co. macellaria* in succession, and also showed little overlap with *C. rufifacies* in the samples. Detailed study of their interaction with the invader is particularly warranted.

Sarcophagid females deposit larvae rather than eggs (Shewell 1987), in contrast to the other species listed here. This strategy gives their larvae a developmental head start at the cost of a great reduction in fecundity. Denno and Cothran (1976) theorized that sarcophagids coexist with the competitively superior calliphorids by more rapidly locating and colonizing smaller carcasses. Our results are at odds with this theory, in that the sarcophagids were not particularly fast at exploiting carrion.

The bionomic similarity between *C. rufifacies* and *Co. macellaria* indicates that their ranges in the New World will be nearly identical (Nicholson 1934; Hall 1948; Bohart and Gressitt 1951; Norris 1959; Denno and Cothran 1975). If these and our previous results may be used to predict the future, then a reduction in *Co. macellaria* density by the invader will be widespread. It appears that by preceding *C. rufifacies* in succession many *Co. macellaria* survive. In fact, except on islands, invaders seldom drive natives to extinction (Vermeij 1991). However, coevolved sets of invading species are thought to have particularly large ecological effects (Simberloff 1991), and *C. rufifacies* was only the first in this genus to

Table 5 Mean and SE of proportional overlap (C_{ih}) within samples for the common taxa of larvae. Values are calculated from carcasses in which both of the taxa in question were collected. The sample size for each is given in parentheses

	Call.	Sarc.	*P. regina*	*Co. macellaria*	*C. rufifacies*
RABBIT CARCASSES					
Call.	–	0.60±0.07 (19)	0.26±0.08 (9)	0.59±0.10 (13)	0.12±0.06 (20)
Sarc.	–	–	0.26±0.11 (7)	0.49±0.11 (11)	0.11±0.05 (19)
P. regina	–	–	–	0.31±0.20 (5)	0.09±0.05 (7)
Co. macellaria	–	–	–	–	0.11±0.06 (13)
GOAT CARCASSES					
Call.	–	0.48±0.06 (22)	0.26±0.05 (10)	0.50±0.06 (23)	0.06±0.01 (24)
Sarc.	–	–	0.09±0.04 (9)	0.37±0.07 (21)	0.07±0.02 (22)
P. regina	–	–	–	0.31±0.07 (10)	0.23±0.09 (10)
Co. macellaria	–	–	–	–	0.08±0.02 (23)

reach North America. *C. megacephala* is sympatric with *C. rufifacies* in the Old World, and now in scattered locations in North, Central and South America (Greenberg 1988; Mariluis and Schnack 1989; Baumgartner 1993). Until recently they did not occur with the other *Chrysomya* now in the New World. Baumgartner and Greenberg (1984) observed the number of adult *Co. macellaria* in their samples drop sharply (at one location from 89 to 0.2% of the total) in Peru following the arrival of historically sympatric *C. albiceps* and *C. putoria.* The interaction of *C. rufifacies* and *C. megacephala,* and their combined effect on North American flies, should be closely studied before their congeners arrive.

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