

Interaction between *Chrysomya rufifacies* and *Cochliomyia macellaria* (Diptera: Calliphoridae): the possible consequences of an invasion

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Abstract

Four Old World blow flies (Diptera: Calliphoridae), *Chrysomya albiceps* (Wiedemann), *C. putoria* Wiedemann, *C. megacephala* (Fabricius), and *C. rufifacies* (Macquart), have recently invaded the New World. The interaction of *Chrysomya rufifacies* (Macquart) with native carrion flies in Texas, USA, was investigated by reducing oviposition by the invader on rabbit carcasses outdoors. These carcasses produced significantly more *Cochliomyia macellaria* (Fabricius) adults compared to carcasses on which the invader was not reduced. The results suggest that *C. macellaria* populations will decline where the two species co-occur. They also support the hypothesis that the carrion community is saturated with species, and provide a mechanism for the possible elimination of *Lucilia caesar* (Linnaeus) in Madeira and the reduction of *C. macellaria* in South America by *Chrysomya albiceps* (Wiedemann).

Introduction

Sarcosaprophagous flies (Calliphoridae and, to a lesser extent, Sarcophagidae) are the principal invertebrate consumers of terrestrial carrion (Braack, 1986; Fuller, 1934; Payne, 1965; Peschke *et al.*, 1977; Putman, 1987; Reed, 1958). Adults are extremely vagile and some species reach a carcass and oviposit within a few hours of death of the animal (Hall, 1948).

Carrion is a patchy and ephemeral resource and the insects that feed upon it rarely complete more than one generation at a carcass (Beaver, 1977). A body of theory suggests that competitors can coexist on a patchy resource provided there is intraspecific aggregation and thus relatively high intraspecific compared to interspecific competition (Atkinson & Shorrocks, 1981; Hanski, 1981; Ives, 1988). It has also been suggested that the carrion ecosystem, although diverse for the reason just given, is structured by intense resource competition, and that as a result such communities are saturated with species (Hanski, 1987). This belief can be tested using an ongoing invasion. Within the last two decades, four

species in the Old World genus *Chrysomya* have been introduced into Latin America (Baumgartner, 1988; Baumgartner & Greenberg, 1984; Laurence, 1986; Olsen & Sidebottom, 1990; Wells, 1991)). The first of these to become established in the continental USA was *Chrysomya rufifacies* (Macquart) which has now been recorded in Texas, Arizona, and California (Baumgartner, 1986; Greenberg, 1988; Richard & Ahrens, 1983). Before this time, *C. rufifacies* was found only in Australasia and the Pacific (James, 1947).

The larvae of *C. rufifacies* are facultative predators on other dipterous larvae (Fuller, 1934). Such a predator/competitor would seem particularly likely to disrupt the native fly fauna. Strong interactions are suggested by studies of *C. rufifacies* in its former range where it has been observed to 'clean a carcass' of other species when food becomes scarce (Bohart & Gressitt, 1951) and to drive other larvae from the food (Fuller, 1934). What is in behavioural terms predation, has been interpreted in ecological terms to be interference competition (Hanski, 1987).

There may be another source of information on how introduced *C. rufifacies* can influence endemic flies. *Chrysomya albiceps* (Wiedemann) has been called the 'biological equivalent' of *C. rufifacies* since the two are extremely

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Table 1. Numbers of each fly species bred from each carcass.

Block	1	1	2	2	3	3	4	4	5	5
Treatment*	1	2	1	2	1	2	1	2	1	2
<i>Chrysomya rufifacies</i> (Macquart)	0	0	0	564	1152	2377	0	6079	0	1233
<i>Cochliomyia macellaria</i> (Fabricius)	0	1436	2308	1130	4407	1097	1571	13	118	53
<i>Phaenicia mexicana</i> (Macquart)	0	0	727	0	0	0	20	0	4	0
<i>Phaenicia sericata</i> (Meigen)	67	0	432	12	0	0	330	0	3	0
<i>Phormia regina</i> (Meigen)	0	135	147	0	0	0	0	0	0	0
Sarcophagidae**	342	452	140	0	0	0	171	0	0	9
<i>Neomuscina tripunctata</i> (Wulp)	0	0	0	0	0	0	0	0	0	17
<i>Muscina stabulans</i> (Fallén)	0	0	0	0	0	0	0	0	13	0
<i>Ophyra aenescens</i> (Wiedemann)	0	0	0	0	0	0	0	0	0	78

*Treatment 1 = ovipositing *C. rufifacies* removed, Treatment 2 = *C. rufifacies* not removed.

**including males of *Sarcophaga bullata* Park and *Blaesoxipha plinthopyga* (Wiedemann), females could not be identified.

similar in both form and behaviour (James, 1947). Hanski (1977) believed that *C. albiceps* introduced in to the island of Madeira caused the extinction of *Lucilia caesar* (Linnaeus). In South America, the density of *Cochliomyia macellaria* (Fabricius) dropped as *Chrysomya* spp. densities increased (Guimarães *et al.*, 1979), a drop that seemed to be greatest where *C. albiceps* was present (Baumgartner & Greenberg, 1984).

The above reports of the ecological impact of *Chrysomya* spp. invasions are quite plausible but do not include actual demonstration of any interaction. Since conclusions about interaction based on distributional data may be in error (Dayton, 1973; Simberloff, 1981), we attempted, through experimental manipulation, to measure the effect of *C. rufifacies* on native flies in North America.

Materials and methods

Carrion flies were allowed to oviposit on freshly thawed rabbit carcasses that had been frozen immediately after death from a blow to the head. Each carcass was held in a disposable aluminium roaster pan with sand 2 cm deep. Carcasses weighed between 1.7 and 2.4 kg and those within a particular block (see below) were within 200 g of each other.

Two study sites were selected on the outskirts of Kerrville, Texas, USA. The terrain and flora of the area are described by Correll & Johnston (1970). Site 1 was a pasture on the grounds of the USDA Knipping-Bushland Livestock Insects Laboratory. Site 2 was a wooded hillside approximately 0.5 km north of site 1. These sites were used in alternating sequence (blocks) from 30.vi.90 through 19.vii.90 beginning with site 2. Daily minimum and maximum air temperatures recorded at the USDA station during this period averaged 19.8°C (15.6–23.3°C) and 32.1°C (22.8–36.1°C), respectively.

The design consisted of three treatments and five blocks. The treatments applied to carcasses were: 1. *Chrysomya rufifacies* adults attracted to the carcass were captured with a battery-powered aspirator (Bioquip Corp., El Segundo, CA). 2. No species were aspirated but the disturbing noise and motion of the investigator from treatment 1 were imitated as closely as possible. 3. The investigator remained at least 10 m from the carcass. Each carcass was exposed to fly activity for 2 h between 07.30–11.30 and 2 h between 15.00–19.00 on each of three

consecutive days (see exception below). When not exposed to flies, each pan was sealed with a cloth and kept in a metal cage that had legs coated with Tangle-Trap (Bioquip Corp., El Segundo, CA) and so was protected from vertebrate and arthropod scavengers. Careful observation was made to see if carrion fly eggs or larvae were deposited through the cloth but none were observed. Treatments 1 and 2 were performed in a sequence that alternated between blocks for each am or pm period on each day (i.e. if the order was 1,2 for am/day 1/block 1, then it was 2,1 for am/day 1/block 2). The original sequence was determined at random. Treatment 3 was performed during the middle of each am and pm period. Due to rainy weather, carcasses from block 5 were left in place for five days in order to achieve the same number (three am, three pm) of exposure periods. Following final exposure, the contents of each roaster pan were emptied into an 18.9 l plastic bucket and covered with 15 cm sawdust. Each bucket was then sealed with a cloth cover and stored in a ventilated building at ambient temperature for at least 30 days before being opened. The number and species of adult flies that emerged within each bucket were recorded. Adult flies were identified using the keys of (Aldrich (1916), Dear (1985), Hall (1948), and by comparison to a reference collection confirmed by systematists from the US National Museum.

We presumed that confining the larvae in a bucket did not increase predation by *C. rufifacies* since in laboratory experiments allowing post-feeding *Cochliomyia macellaria* to escape from sawdust-filled rearing jars did not decrease mortality from *Chrysomya rufifacies* (Wells & Greenberg, unpublished data).

Results

The adult flies bred from each container are listed in table 1. Several of the samples from treatment 3 were found to have been destroyed by dermestid beetles so that treatment was dropped from the analysis. Block 1 did not produce any *Chrysomya rufifacies* and so was also of no use for this study. Although some *C. rufifacies* emerged from treatment 1 in block 3 it is clear that *C. rufifacies* numbers were sharply reduced by the exclusion technique. Analysis of the data was confined to the numbers of *Cochliomyia macellaria* since only that native species emerged from every block. Fly counts were sub-

mean number of adults

Fig. 1. Response of *Cochliomyia macellaria* to treatment 1.

jected to the t-test for paired number of *C. macellaria*. Block 1 was significant ($\alpha = 0.5$, 3 df) and *Cochliomyia macellaria* is shown in figure 1.

These results reduce *Cochliomyia macellaria* and support the role of *Chrysomya albiceps* in Madeira and

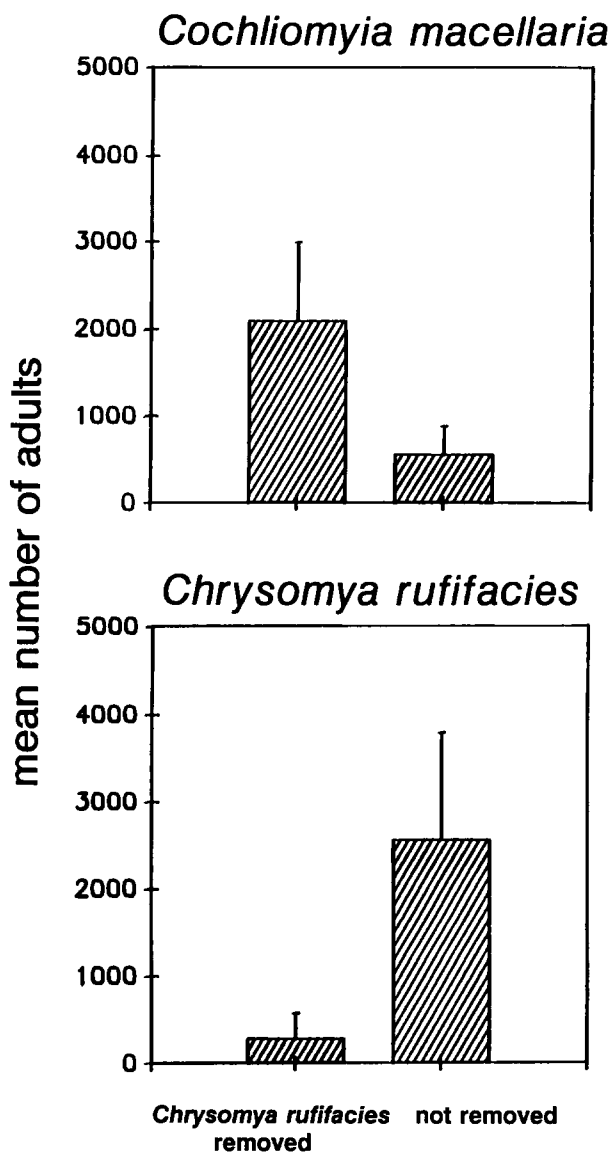


Fig. 1. Response of the numbers of adult *Chrysomya rufifacies* and *Cochliomyia macellaria* adults bred from rabbit carcasses, to the removal of ovipositing *Chrysomya rufifacies*.

jected to the square root transformation and a one-tailed t-test for paired comparisons (Sokal & Rohlf, 1981). The number of *C. macellaria* bred from carcasses in treatment 1 was significantly higher than in treatment 2 ($t = 2.8$, $\alpha = 0.5$, 3 df). The mean numbers of *Chrysomya rufifacies* and *Cochliomyia macellaria* from each treatment are shown in fig. 1.

Discussion

These results suggest that *Chrysomya rufifacies* could reduce *Cochliomyia macellaria* density in the study area, and support hypotheses that the closely related *Chrysomya albiceps* has negatively affected *Lucilia caesar* in Madeira and *Cochliomyia macellaria* in South America. If

one accepts *Chrysomya rufifacies* as a competitor of *Cochliomyia macellaria* then these results also suggest that the carrion community studied is indeed saturated with competing species. Since the food requirements, temperature tolerances and seasonal behaviour of the *Chrysomya rufifacies* and *Cochliomyia macellaria* are similar (Bohart & Gressitt, 1951; Das *et al.*, 1979; Denno & Cothran, 1975; Hall, 1948; James, 1947; Nicholson, 1934; Norris, 1959), there should be considerable geographical and ecological overlap between them. We anticipate a reduction in *Cochliomyia macellaria* density over a wide area of North America.

Concern has been expressed about the economic impact of this invasion (Schmidt & Kunz, 1985). *Chrysomya rufifacies* is a serious parasite of newborn calves in extremely wet areas of Hawaii (Shishido & Hardy, 1969) and may aggravate wounds already infested with other Diptera (Zumpt, 1965). So far, however, myiasis cases involving *C. rufifacies* comprise only 11 out of 2351 samples submitted since 1981 to the USDA National Veterinary Services Laboratories in Ames, Iowa (J.L. Schlater, pers. comm.), and this species is a relatively unimportant vector of enteric disease (Bohart & Gressitt, 1951).

The applied importance of *C. rufifacies* may be greatest in forensic entomology. This species has been useful for homicide investigations in Hawaii (Goff & Odum, 1986; Goff *et al.*, 1986). In its new range, *C. rufifacies* larvae were recovered from human cadavers in Costa Rica (Jirón, 1979) and California (Greenberg, 1988), and one of us (J.D.W.) has encountered *C. rufifacies* from a homicide victim in Tucson, Arizona.

The general pattern of calliphorid invasions around the world is familiar for many taxa. We are aware of thirteen species found in the New World (excluding islands) that are known or thought to be introduced from the Old World (four *Chrysomya* spp., four *Pollenia* spp. (N.P. Wyatt pers. comm.) (the taxonomy of the *Pollenia* spp. is in a state of flux (K. Rognes, pers. comm.) and conclusions about their biogeography may change), two *Bellardia* spp. (Shewell, 1987), *Aldrichina grahami* (Aldrich) (James, 1953), *Calliphora vomitoria* (Linnaeus) (Hall, 1948), *Lucilia sericata* (Meigen) (Aubertin, 1933) but only one introduction (*Cochliomyia hominivorax* (Coquerel) (Palca, 1990)) in the opposite direction. Blow flies strongly fit the net 'east to west' movement of many taxonomic groups (di Castri, 1989).

One may speculate why so many *Chrysomya* spp. have successfully colonized the western hemisphere during such an apparently short period of time. This coincidence seems even more unlikely considering that *C. albiceps* and *C. rufifacies* are monogenic (females produce offspring of a single sex) (Ullerich, 1976) and, from a purely genetic standpoint, poor colonizers (Barrett & Richardson, 1986). The number of insects, including blow flies, transported by humans to new areas must be tremendous. *Chrysomya* spp. have been intercepted in passenger luggage from the Old World at USA airports (Gagné *et al.*, 1982). Although the source of the Brazilian *Chrysomya* spp. may have been identified (Guimarães *et al.*, 1979) the question remains as to why these introductions were a success. In fact, an examination of museum specimens revealed that *Chrysomya* spp. occurred in the New World, but apparently did not become established,

as far back as the 1800s (Baumgartner & Greenberg, 1984). It is tempting to suppose that the increase in human commerce and growth in urban centres, with new opportunities for synanthropic flies (Greenberg, 1971) has paved the way for these invaders.

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References

- Aldrich, J.M. (1916) *Sarcophaga and allies in North America*. 301 pp. La Fayette, Indiana, Thomas Say Foundation.
- Atkinson, W.D. & Shorrock, B. (1981) Competition on a divided and ephemeral resource: a simulation model. *Journal of Animal Ecology* **50**, 461-471.
- Aubertin, D. (1933) Revision of the genus *Lucilia* R.-D. (Diptera, Calliphoridae). *Zoological Journal of the Linnaean Society* **38**, 389-436.
- Baumgartner, D.L. (1986) The hairy maggot blow fly, *Chrysomya rufifacies* (Macquart) confirmed in Arizona. *Journal of Entomological Science* **21**, 130-132.
- Baumgartner, D.L. (1988) Spread of introduced *Chrysomya* blowflies (Diptera: Calliphoridae) in the Neotropics with records new to Venezuela. *Biotropica* **20**, 167-168.
- Baumgartner, D.L. & Greenberg, B. (1984) The genus *Chrysomya* (Diptera: Calliphoridae) in the New World. *Journal of Medical Entomology* **21**, 105-113.
- Barrett, S.C.H. & Richardson, B.J. (1986) Genetic attributes of invading species. pp. 21-33 in Groves, R.H. & Burdon, J.J. (Eds) *Ecology of biological invasions*. Cambridge University Press.
- Beaver, R.A. (1977) Non-equilibrium 'island' communities: Diptera breeding in dead snails. *Journal of Animal Ecology* **46**, 783-798.
- Bohart, G.E. & Gressitt, J.L. (1951) Filth-inhabiting flies of Guam. *Bulletin of the Bernice P. Bishop Museum* **204**, 1-169.
- Braack, L.E.O. (1986) Arthropods associated with carcasses in the northern Kruger National Park. *Suid-Afrikaanse Tydskrif vir Natuurnavorsing* **16**, 91-98.
- di Castri, F. (1989) History of biological invasions with special emphasis on the Old World. pp. 1-30 in Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H.F., Kruger, J., Rejmanek, M. & Williamson, M. (Eds) *Biological invasions*. New York, John Wiley & Sons.
- Correll, D.S. & Johnston, M.C. (1970) *Manual of the vascular plants of Texas*. 1881 pp. Reiner, Tx, Texas Research Foundation.
- Das, S.K., Roy, R. & Dasgupta, B. (1979) The diurnal activity of *Chrysomya rufifacies* Macquart (Diptera: Calliphoridae) in Calcutta, India. *Oriental Insects* **13**, 149-154.
- Dayton, P.K. (1973) Two cases of resource partitioning in an intertidal community: making the right prediction for the wrong reason. *American Naturalist* **107**, 662-670.
- Dear, J.P. (1985) A revision of the New World *Chrysomyini* (Diptera: Calliphoridae). *Revista Brasileira de Zoologia* **3**, 109-169.
- Denno, R.F. & Cothran, W.R. (1975) Niche relationships in a guild of necrophagous flies. *Annals of the Entomological Society of America* **68**, 741-754.
- Fuller, M.E. (1934) The insect inhabitants of carrion: a study in animal ecology. *Council for Scientific and Industrial Research Bulletin (Australia)* **82**, 4-63.
- Gagné, R.J., Gerrish, R.R. & Richard, R.D. (1982) Correspondence. *Entomological Society of America Newsletter* **5**, 9.
- Goff, M.L. & Odum, C.B. (1987) Forensic entomology in the Hawaiian Islands. *American Journal of Forensic Medicine and Pathology* **8**, 45-50.
- Goff, M.L., Odum, C.D. & Early, M. (1986) Estimation of post-mortem interval by entomological techniques: a case study from Oahu, Hawaii. *Bulletin of the Society of Vector Ecologists* **11**, 242-246.
- Greenberg, B. (1971) *Flies and disease*. Vol. 1. 856 pp. Princeton University Press.
- Greenberg, B. (1988) *Chrysomya megacephala* (F.) (Diptera: Calliphoridae) collected in North America and notes on *Chrysomya* species present in the New World. *Journal of Medical Entomology* **25**, 199-200.
- Guimarães, J., do Prado, A. & Buralli, G. (1979) Dispersal and distribution of three newly introduced species of *Chrysomya* Robineau-Desvoidy in Brazil (Diptera: Calliphoridae). *Revista Brasileira Entomologia* **23**, 245-255.
- Hall, D.G. (1948) *The blow flies of North America*. 477 pp. Thomas Say Foundation. Lafayette, Indiana, USA.
- Hanski, I. (1977) Biogeography and ecology of carrion flies in the Canary Islands. *Annales Entomologici Fennici* **43**, 101-107.
- Hanski, I. (1981) Coexistence of competitors in patchy environments with and without predation. *Oikos* **37**, 311-321.
- Hanski, I. (1987) Nutritional ecology of dung- and carrion-feeding insects. pp. 837-884 in Slansky, F. & Rodriguez, F.G. (Eds) *Nutritional ecology of insects, mites, spiders and related invertebrates*. New York, John Wiley and Sons.
- Ives, A.R. (1988) Aggregation and the coexistence of competitors. *Annales Zoologici Fennici* **25**, 75-88.
- James, M.T. (1947) The flies that cause myiasis in man. *Miscellaneous Publications. United States Department of Agriculture* **631**, 1-175.
- James, M.T. (1953) Notes on the distribution, systematic position, and variation of some Calliphorinae, with particular reference to the species of western North America. *Proceedings of the Entomological Society of Washington* **55**, 143-148.
- Jirón, L.F. (1979) Sobre moscas californidas de Costa Rica (Diptera: Cyclorrhapha). *Brenesia* **16**, 221-222.
- Laurence, B.R. (1986) Old World blow flies in the New World. *Parasitology Today* **2**, 77-79.
- Nicholson, A.J. (1934) The influence of temperature on the activity of sheep-blowflies. *Bulletin of Entomological Research* **25**, 85-99.
- Norris, K.R. (1959) The ecology of sheep blowflies in Australia. *Monographiae Biologicae* **8**, 514-544.
- Olsen, A.R. & Sidebottom, T.H. (1990) Biological observations on *Chrysomya megacephala* (Fabr.) (Diptera: Calliphoridae)

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Pacific Entomologist* 66, 126-130.
- Palca, J.** (1990) Libya gets unwelcome visitor from the west. *Science* 249, 117-118.
- Payne, J.A.** (1965) A summer study of the baby pig, *Sus scrofa* Linnaeus. *Ecology* 46, 592-602.
- Peschke, K., Krapf, D. & Fuldner, D.** (1987) Ecological separation, functional relationships, and limiting resources in a carrion insect community. *Zoologische Jahrbücher für Systematik Oekologie und Geographie der Tiere* 114, 241-265.
- Putman, R.J.** (1977) Dynamics of the blowfly, *Calliphora erythrocephala*, within carrion. *Journal of Animal Ecology* 46, 853-866.
- Reed, H.B.** (1958) A study of dog carcasses in Tennessee, with special reference to the insects. *American Midland Naturalist* 59, 213-245.
- Richard, R.D. & Ahrens, E.H.** (1983) New distribution record for the recently introduced blow fly *Chrysomya rufifacies* (Macquart) in North America. *Southwestern Entomologist* 8, 216-218.
- Schmidt, C.D. & Kunz, S.E.** (1985) Reproduction of *Chrysomya rufifacies* in the laboratory. *Southwestern Entomologist* 10, 163-165.
- Shewell, G.E.** (1987) Calliphoridae. pp. 1133-1145 in McAlpine, J.F. (Ed.) *Manual of Nearctic Diptera*. Research Branch, Agriculture Canada, Ottawa.
- Shishido, W.H. & Hardy, D.E.** (1969) Myiasis of new-born calves in Hawaii. *Proceedings of the Hawaiian Entomological Society* 20, 435-438.
- Simberloff, D.S.** (1981) Community effects of introduced species. pp. 53-81 in Nitecki, M. *Biotic crises in ecological and evolutionary time*. New York, Academic Press.
- Sokal, R.R. & Rohlf, F.J.** (1981) *Biometry*. 859 pp. New York, W.H. Freeman and Co.
- Ullerich, F.-H.** (1976) Chromosomenverhältnisse, konstitutes Heterochromatin und Geschlechtbestimmung bei einigen Arten der Gattung *Chrysomya* (Calliphoridae, Diptera). *Chromosoma* 58, 113-136.
- Wells, J.D.** (1991) *Chrysomya megacephala* (Diptera: Calliphoridae) has reached the continental United States: a review of its biology, pest status, and spread around the world. *Journal of Medical Entomology* 28, 471-473.
- Zumpt, F.** (1965) *Myiasis in man and animals in the Old World*. 267 pp. London, Butterworths.

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