Biogeography and ecology of carrion flies in the Canary Islands

Ilkka Hanski


Four species of calliphorids, Lucilia sericata, Calliphora splendens, C. vicii, and C. vomitoria, have been present in the Canary Islands during the last 150 years, while Chrysomya albiceps has certainly been observed since the beginning of this century. An additional species, Chrysomya chloropyga, is now recorded. Nearly in Madeira, Lucilia caesar has become extinct and there has been an invasion by C. albiceps. The low number of Lucilia/Chrysomya species coexisting in these islands is attributed to interspecific competition, the possible ultimate causes including low habitat diversity and lack of seasonality in the climate.

Three questions require further study: (1) The fate of the C. chloropyga population should be followed, (2) The rate of immigration of calliphorids with ships and aeroplanes should be assessed, (3) The position of sarcophagids in the carrion fly community deserves special attention, because their reproductive strategy is different from that of the Lucilia/Chrysomya species, and they are possibly unusually numerous in the Canaries.

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The current interest in island biogeography, initiated by the pioneering theoretical work of MacArthur & Wilson (1967), has largely been stimulated by studies on birds. Some features of birds and their communities make them particularly suitable for such work. Censusing is relatively simple and accurate; they form an apparently natural group of animals, and a group of suitable size; and more or less reliable past records are frequently available. Flies breeding on carrion resemble birds in these respects. Characteristically, their community consists of species more or less ecologically isolated from other animals. The number of species is low, and censusing is, at least in principle, rapid and accurate, even without breeding experiments (which are simple to carry out. e.g. Hanski 1976). The relation between the productivity and utilization of the environmental resources is exceptionally straightforward: populations are strictly food-limited, in the sense that they consume all the food available without delay. But, since they cannot (usually) influence the rate of carrion production, they cannot “overexploit” their environment, i.e. decrease its productivity. Blowflies, the core of the community, have already attracted the interest of ecologists (not to mention students of applied entomology). Therefore, it seems appropriate to pay attention to the island ecology of carrion flies, partly in the hope of increasing our understanding of their ecology in general.

I collected carrion flies during one month, from December 1976 to January 1977, in Tenerife, La Gomera, and Fuerteventura, three of the seven oceanic Canary Islands. Employing fish and liver baits, I covered all the naiiru habitats, which ranged from the semi-desert in Fuerteventura to the evergreen forest in La Gornera and Tenerife to the subalpine zone of Tenerife. Previous taxonomic-faunistic knowledge on the Canarian flies in the family Calliphoridae has been summarized by Baez & Santos-Pinto (1973); older sources of information include hfacquart’s list of 107 species of Diptera in Webb & Berthelot (1839). A recent book edited by Kunkel (1976) reflects the current knowledge of the biogeography and ecology of
various organisms in the Canary Islands, and finally, an entomological bibliography of the Canaries is now available (Machado 1976e).

In this paper I shall describe the structure of the carrion fly community in the Canaries, give an account of their habitat selection, and briefly review past observations. The biogeographical and ecological implications will be discussed, and some further work suggested.

The community of carrion flies

Flies breeding and feeding on carrion include specialist species, more or less confined to the carrion microhabitat, and generalists, breeding in other microhabitats besides carrion. At least quantitative differences in the preference of different types of carrion may also occur (e.g. Novotny 1963). A great number of other fly species also feed only on carrion, but rarely or never breed on it (e.g. Hanski 1976). In the Canary Islands the present species composition is:

1) Specialists. The following species may be included in this category: Lucilia sericata Meig., Chrysomya albiceps Wied., C. chloropyga Wino., Calliphora splendens Macq., C. vicina Rob. Desv., and C. vomitoria L. Of these C. albiceps at least may also breed in other decomposing matter, e.g. in pig manure (M. Baez, pers. comm.), but carrion may be regarded as its main food resource.

C. chloropyga has not been reported earlier from the Canary Islands. After my discovery, Mr. M. Baez kindly checked the Chrysomya material in the Museum of Santa Cruz (Tenerife), and found a specimen of C. chloropyga collected from a ship in the port of Santa Cruz in 1947 (the ship was coming from Fernando Poo). What is even more interesting, Baez told me of the following new records recently made by him: February 1977, several specimens on Fuerteventura near small villages; April 1977, two specimens at San Andrés (Tenerife); and 20–25 April, one specimen in Lanzarote, in a restaurant. Therefore, C. chloropyga evidently belongs to the current fauna of the Canary Islands, but in view of the quality and quantity of previous collecting, it may be assumed to have been absent or very rare until recently.

2) Generalists. Species of the genera Muscina, Synthesiomyia and Sarcophaga (s.l.) appear to belong to this group; at least many of them may be carrion-inhabiting (Emden 1954, Hanski 1955–64). Canarian species are: Muscina stabulans Fall. (T, F, G), M. estillalis Fall. (T), M. populorum Taban. (T), Synthesiomyia nudicola Wulp (T, F, G), Sarcophaga haemorrhoidalis Meig. (T, F, G), S. jatulista Fries & S. crassipalpis Macq. (T, F), S. exuberans Pand., S. tricolor Vill., S. oeceri Vill., S. melanophila Vill., S. ferox Vill. (F), S. albopunctata Vill., S. hyalina Pand., S. pallida Meig., S. tibialis Macq. (T, F, G), S. haemorrhoidalis Bött., S. hirticollis Wied., S. punila Meig., S. albiceps Coll., S. lutea Coll., S. vespertilio Coll., S. olivacea Coll., and S. fuliginosa Coll. (and Schizophora latifrons Fall. (T, F, G)). In addition, three probably undescribed species (Sarcophaga sp. (s.s.), Bellera sp. and Pierretia sp.; J. Dear, in litt.). Species treated as an asterisk are known from the work of Frey (1937) and Baez (unpubl.), but were not included in my collection (not carrion-inhabiting?). As knowledge on the sarcophagid fauna is especially scanty and the biology of many species is not well known, I have listed here only to present my own observations, and to call attention to the (high) number of species visiting carrion. The abbreviations for the islands are: T = Tenerife, F = Fuerteventura and G = La Gomera.

3) Species feeding (but not breeding) on carrion were not included in the present study. Many muscids (e.g. five Musca species) belong to this group in the Canary Islands.

Habitat selection

Of the specialist species, L. sericata predominates in all exposed habitats at low altitudes (my data are presented in Table 1). At high altitudes it is probably very scarce, because I did not catch a single individual above ca. 500 m, but it has been found earlier in the subalpine zone in Tenerife (Baez & Santos-Pinto 1975). My collection is not large enough to allow definite conclusions and it was obtained during only one season but previous information suggests that there is little, if any, seasonal variation in the species composition (Frey 1937, Baez & Santos-Pinto 1975). Chrysomya albiceps is also restricted to open habitats at low altitudes, and co-occurs with L. sericata, most probably being completely included within the habitat range of the latter. As already mentioned, C. albiceps may live in other decomposing matter besides carrion. Chrysomya chloropyga is
Table 1.

Numbers of calliphorids collected between 21 December 1976 and 10 January 1977 from Tenerife, La Gomera and Fuerteventura. The total number of individuals was over 2400. The places are the following: Tenerife: 1 = La Florida, ca. 700 m above sea level, open meadow; 2 = La Florida, ca. 700 m, mixed forest; 3 = Puerto de la Cruz, ca. 20 m, town; 4 = Aguamansa, ca. 1300 m, open scrub; 5 = Ml Teide, ca. 2300 m, sparse scrub; 6 = Icod, ca. 20 m, open scrub; 7 = Candelaria, ca. 20 m, open scrub; 8 = La Laguna, ca. 500 m, town; 9 = Los Cristianos, ca. 20 m, coast; 10 = Santa Cruz, ca. 20 m, rubbish dump; 11 = San Andrés, ca. 20 m, village; 12 = Vilaflor, ca. 1300 m, pine forest; 13 = La Guancha, ca. 500 m, village; 14 = La Guarcha, ca. 900 m, open meadow; 15 = La Guancha, ca. 1000 m, mixed forest. La Gomera: 16 = El Cedro, ca. 1300 m, laurisilva; 17 = Hermigua, ca. 20 m, coast; 18 = San Sebastian, ca. 20 m village. Fuerteventura: 19 = Puerto del Rosario, ca. 20 m, coast; 20 = Tinejita, ca. 100 m, semi-desert; 21 = Gran Tarajal, ca. 20 m, village; 22 = Pd de Jandia, ca. 20 m, coast; 23 = Pd de Jandia, ca. 50 m, semi-desert; 24 = Casillas, ca. 100 m, village; 26 = Casillas, ca. 400 m, hill; 27 = Airport, ca. 20 m, coast. Figures give the numbers of males/females.

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most probably a recent colonist of the Canaries, and (still) rare.

The three Calliphora species form an interesting group. C. splendens, an endemic Canarian calliphorid, is a habitat specialist; its typical macrohabitat is the high altitude (400 to 1300 m, Bramwell & Bramwell 1971) evergreen laurisilva forest (Machado 1976b), but I also found it in a very small deciduous wood (a remnant of previous laurisilva forest? La Florida, Tenerife). In contrast, C. vicina is an extreme macrohabitat generalist: it was found in every habitat where flies were collected, from the semi-desert to the subalpine scrub to the
laurisilva forest. In the open habitats it occurs only in small numbers, while it attains its maximum abundance in the pine and mixed forest, where it predominates. The third calliphorid, Lucilia vomitoria, seems to be very scarce everywhere, and is probably confined to forests (mixed and laurisilva), where it is always outnumbered by C. vicina and/or C. splendens. The occurrence of C. vomitoria in the town of La Laguna (Tenerife) may be due to transport, because the flies were collected from a small rubbish dump consisting of vegetable matter.

Historical evidence

Information on the carrion flies of the Canary Islands is available from three old sources: MACQUART (1839), BECKER (1908a) and FREY (1937). If we assume that carrion flies have approximately 10 generations every year in the Canaries (cf. e.g. HANSKI 1976), the records date back ca. 1400, 630 and 400 generations, respectively. These figures may be somewhat too high for the Calliphora species, which mainly occur at higher altitudes, where temperatures are lower, but in any case, the time span covered is substantial from the flies' point of view. Table 2 summarizes the knowledge on the true carrion specialists.

All the three Calliphora species have been present throughout the period covered and the species abundance relations have been much the same as they are nowadays, at least during this century (see BAEZ & SANTOS-PINTO 1973): C. vicina is common, C. vomitoria is rare, and C. splendens restricted to the laurisilva, where it predominates. The Lucilia and Chrysomyia species show some changes. L. scerica, which has obviously occurred in the Canaries during the whole period of 150 years, is the only Lucilia species recorded in this century, which makes Macquart's report of L. caesar particularly interesting. Unfortunately, it is not possible to check the identification, because a large part of the material recorded by Macquart from the Canaries has been lost, probably during one of the disastrous floods of the Seine in the 19th century. MACQUART (1839: 114) wrote of "L. caesar", "Espèce des plus communes dans toute l'Europe et le nord de l'Afrique". This does not fit C. albiceps, a northern African and southern European species, but, as shown by AUBERTIN (1933), Macquart was not able to identify Lucilia species correctly. Therefore, the identity of Macquart's "L. caesar" from the Canaries can probably never be solved. It may have been L. caesar, or some other Lucilia, and it is even possible that it was C. albiceps.

Apart from the sarcophagids, the only facultative carrion fly listed by MACQUART (1839) was Curtonervia (Musca) stabulans. However, it is doubtful whether other species were actually lacking; they may just have been uncommon or overlooked. BECKER (1908b) observed M. assimilis and M. stabulans, and FREY (1937) added M. pabulorum and Synthesiomyia nudiseta. As at least some of these species are more or less synanthropic, it is, of course, possible that the number of species has really increased.
Discussion

The absence of all *Lucilia* species other than *L. sericata* from the Canary Islands is unexpected: the size of the islands is considerable (Tenerife over 2,000 km²), and they are not far from the African continent (Fuerteventura and Gran Canaria 100—130 km). In view of their geographical distribution, it would not be surprising to find *Lucilia ampullacea* Vill., *L. bufo nitor* Mon., *L. richardi* Collin, *L. silvarum* Réig. or *L. cuprina* Wied. In particular, the absence of *L. caesar* is puzzling, because it occurs in both southern Europe and northern Africa, as well as on the Mediterranean islands (*Aubertin 1933*). *Chrysomya albiceps* presumably has an ecological role roughly similar to that of the *Lucilia* species.

Luckily, historical information is available from Madeira nearby which, though smaller and more oceanic, is otherwise rather similar. At the beginning of this century, Becker (1908b) observed *L. caesar*, *L. sericata* and *C. vicina*, while 70 years later, Baez & Santos-Pinto (1975) listed *L. sericata*, *C. albiceps*, *C. vicina* and *C. vomitoria*. The omission of *C. vomitoria* from Becker's publication may be due to its absence or its rarity; the absence of *C. splendens* is not due to the lack of suitable habitats. But the exciting point is the apparent extinction of *L. caesar*, and the invasion by *C. albiceps*.

It seems that the most likely explanation of the impoverished calliphorid fauna of the Canaries and hfaideira is intense interspecific competition. The invasion of Madeira (and possibly earlier of the Canaries) by *C. albiceps* may be due to the improved opportunities for immigration offered by human transport, whereas the (subsequent?) extirpation of *L. caesar* could be attributed to competitive exclusion. Seguy (1928) reported that *L. caesar* is often less frequent when occurring with *L. sericata* and *L. cuprina*. The current situation: (1-3) *Lucilia/Chrysomya* species in both the Canaries and hfaideira: appears to be the equilibrium number of species in the present environment of the islands. Ultimately, low species diversity may be due to low habitat diversity. But contributory factors may be the limited area, low carrion production and a low immigration rate. The carrion production in the Canary Islands is probably lower than on the mainland; it consists mainly of birds, fish, rabbits and lizards, nowadays enriched by two species of introduced rats. And finally, the lack of seasonality in the climate makes the environment more homogeneous in time, which might result in a decrease in species diversity.

Two suggestions may be made for further study. Attention should be paid to the fate of the newly discovered *C. chloropyga* population (or populations, because at least three islands are involved). Secondly, it would be interesting to obtain information about the rate of immigration of (other) *Lucilia* and *Chrysomya* species with ships and aeroplanes. Such immigration must surely occur. The rate of "natural" immigration may be low, because of the prevailing Atlantic winds.

The similarity of the species composition in the Canaries, and Madeira, and on the different islands in the Canaries, supports Lack's (1976) view of island biogeography, rather than the concept of a dynamic equilibrium biota, in the sense of MacArthur & Wilson (1967). A survey of the collections in the British Museum (Natural History) revealed that *L. sericata*, a truly cosmopolitan species, has also been a successful island colonist outside the Canaries and hfaideira. The list of its conquests includes Azore, St. Helena, Gough Is., Tristan da Cunha, Cypros, hfaideira, Great Salvage Is., Cape Verde Is., Henderson Is., Rapa Is. (S. Pacific) and Hawaii. Of the other *Lucilia* species, *L. cuprina* (a close relative of *L. sericata*) and *L. papuensis* Macq. show similar behaviour in the southern hemisphere, and a number of species are endemic to different oceanic islands: e.g. *Lucilia aureovulvata* Theowald (Solomon Is.) and *L. andrewsi* Senior-M'hite, Aubertin & Sриart (Christmas Is.) (British Museum, Natural History).
cording to James (1966), the Galapagos Islands are inhabited by no less than three endemic Lucilia species besides one widespread calliphorid, a situation similar to that in Hawaii and in the West Indies (James 1967, 1971). It is interesting that L. cuprina seems to be replacing L. sericata in Madagascar and other Indian Ocean islands (J. Dear, in litt.).

The Canarian Calliphora species seem to have retained their respective positions during the last 150 years. C. splendens, the only endemic Canarian calliphorid, and most probably derived from C. vicina or C. vomitoria, is another example of high altitude endemism in island animals (see Lack 1976 for evidence and argument concerning birds).1 Another interesting point in the Calliphora group is the relation between C. vicina and C. vomitoria: the niche realized by the latter is apparently included within that of the former, and C. vicina always seems to predominate over C. vomitoria. This could be neatly explained by the patchy distribution of their resources; the general theory predicts that this situation allows more than one similar species to coexist (e.g. Horn & MacArthur 1972, Slatkin 1974, see also Hanski 1977a). But why then, one may ask, is the coexistence of two or three species more difficult or impossible in open habitats at low altitudes? After analysing a model that was reasonably realistic for the carrion community, I argued (Hanski 1977b) that, regardless of the patchy distribution of their food resource, the question of the coexistence of similar species competing exploitatively (such as carrion flies) is still a problem. In particular, I predicted that when the rate of development increase, diversity may be expected to decrease rather than to in-

crease. The pattern in the calliphorid community in the Canaries fits this prediction (forest habitats have a cooler microclimate, and hence a lower rate of maturation in the carrion community), but, of course, other factors may be involved.

A third question that might repay further study is the relation between Lucilia and Sarcophaga species in the Canaries. The general background is that they represent two distinct reproductive strategies: Lucilia females lay up to several hundred eggs at a time, while Sarcophaga females lay one or a few living larvae. Denno & Cootran (1976) list some other separating characteristics and conclude that "they [Lucilia and Sarcophaga spp.] evolved very different but equally opportunistic ("r-selected") strategies of carrion exploitation". But here the puzzling fact is that Lucilia species are often superabundant, while Sarcophaga species are always much more uncommon. Therefore, one wonders why a "Lucilia mutant" of a Sarcophaga does not appear, and rapidly display the superiority of its life history over the original one. The explanation may lie in the predation on eggs and small larvae, which is extremely high in the carrion community (e.g. Nuorteva 1970, Hanski 1976), and in competition between larvae. Sarcophaga larvae will evidently have an immediate advantage over Lucilia larvae, being able to start their development earlier. In any case: the fitness of a newly laid Sarcophaga larva must exceed the fitness of a Lucilia egg, and presumably, the fitnesses of Lucilia and Sarcophaga females represent two adaptive "peaks". But the specific explanation of the existence of the "inferior" Sarcophaga strategy is unclear.

It would be interesting to obtain answers to the following questions: Is the relative importance of the sarcophagids greater in the carrion community in the Canaries than, say, in Europe? There is evidence that this is the case (for Finland see Hanski 1976, Hanski & Kuusela 1977, and for N. America see Denno & Cootran 1976). What is the role of egg and larvae

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1Frey (1937) gives the following figures for the endemic proportion of the whole dipterous fauna at different altitudes: coastal areas, 40.0 %; arid zone (low altitude), 30.5 %; forest zone (middle altitude), 39.5 %; and subalpine zone (high altitude), 34.0 %. Thus, there are no differences between the zones, and it seems probable that the "high altitude endemism" may reflect particular rather than general ecological and evolutionary relations.
predators in the Canaries? Is the average size of a piece of carrion smaller in the Canaries than in Europe? Naturally, these and similar questions are not confined to the Canary Islands.

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