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Spatial and temporal habitat partitioning by calliphorid blowflies

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Abstract. Blowflies (Diptera: Calliphoridae) perform an essential ecosystem service in the consumption, recycling and dispersion of carrion nutrients and are considered amongst the most important functional groups in an ecosystem. Some species are of economic importance as facultative agents of livestock myiasis. The interspecific ecological differences that facilitate coexistence within the blowfly community are not fully understood. The aim of this work, was to quantify differences in habitat use by calliphorid species. Thirty traps were distributed between 3 habitats in 2 sites in south west England, collections were made from March to August of 2016. A total of 17,246 specimens were caught, of which 2,427 were *L. sericata*, 51 *L. richardsi*, 6,580 *L. caesar*, 307 *L. ampullacea*, 4,881 *C. vicina* and 2,959 *C. vomitoria*. *L. sericata*, was the dominant species in open habitats, whereas *L. caesar*, was the most abundant species in shaded habitats. *Calliphora* specimens were more abundant in the cooler months. It is suggested that *Calliphora* and *Lucilia* show strong temporal segregation mediated by temperature whereas habitat use differences within species of the genus *Lucilia* are likely to be driven by differences in humidity tolerance and light intensity, resulting in effective niche partitioning.

Key words: blowfly, competition, decomposer, habitat, microclimate, niche, temperature, humidity, *Lucilia*, *Calliphora*,

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Introduction

The Calliphoridae is a family of cyclorrhaphan Diptera which contains more than 1000 species in about 150 genera worldwide (Rognes, 1991). Arthropods perform an essential ecosystem service in the consumption, recycling and dispersion of carrion nutrients (Putman, 1983; Parmenter and MacMahon, 2009). Sarcosaprophagous flies (including Calliphoridae and Sarcophagidae) are considered to be the principal invertebrate consumers of terrestrial carrion (Peschke *et al.*, 1987) and in this role they have a major ecological significance. Some blowflies have also evolved ectoparasitic behaviour, known as myiasis and their larvae can infest living animals and live in the host's living or necrotic tissue (Zumpt, 1965).

In Northern Europe, *Lucilia sericata* (Diptera:Calliphoridae) (Meigen) is considered to be the most economically important calliphorid species, as it is the primary myiasis agent involved in sheep flystrike cases (MacLeod, 1943; Wall *et al.*, 1992), however it also has an important role in carrion decomposition and **has** been reported emerging from carcasses in the field (Lane, 1975; Blackith and Blackith, 1990; Smith and Wall, 1997). Despite the fact that *L. sericata* is the most important myiasis-causing species in countries such as the UK, it is mainly saprophagous in other countries, as the case in Spain, where the most important agent of sheep myiasis is the fleshfly *Wohlfahrtia magnifica* (Diptera:Sarcophagidae) (Schiner) and *L. sericata*, although abundant acts largely as a necrophagous species (Ruíz-Martínez *et al.*, 1992; Ruíz-Martínez *et al.*, 1993). In Finland *L. sericata* is reported as a species of low abundance (Hanski and Kuusela, 1977) with *Lucilia illustris* (Diptera:Calliphoridae) (Meigen) the being most abundant species in the carrion fly community. In Scotland *Lucilia caesar* (Diptera:Calliphoridae) (Linnaeus) is more commonly involved in sheep myiasis (Morris and Titchener, 1994), whereas in England it is mainly saprophagous (Smith and Wall, 1997b) and it has been rarely reported as a primary myiasis agent (Wall *et al.*, 1992a). Another blowfly present in the UK, *Lucilia richardsi* (Diptera:Calliphoridae) (Collin) is sympatric with *L. sericata* in many parts of its range; it is genetically closely related to *L. sericata* (McDonagh and Stevens, 2011; Arias-Robledo *et al.*, 2018) and also morphologically almost identical, differing externally only by the presence of one additional seta on the tibia of the middle leg (Aubertin, 1933). However, it is a species that has been poorly studied and, regardless of the similarity with its sister species, *L. sericata*, it has never been recorded from sheep strike cases. (Wall *et al.*, 1992a). The cause of the differences in abundance and behaviour of various calliphorid blowfly species in different areas, remains unclear.

Carrion is an ephemeral resource and the insect community that feed upon it rarely complete more than one generation in a single carcass (Beaver, 1997). It has been suggested that the carrion ecosystem is structured by intense resource competition, and that carrion communities are saturated with species (Hanski, 1987). Hence, it might be expected that clear ecophysiological, behavioural or phenological differences would be seen among species that share this ecosystem to allow niche partitioning in space and time. Studies have shown that the blowfly species composition may be influenced by factors such as size, species and age of carcass (Smith and Wall, 1997a,b.; Blackith and

Blackith, 1990; Davies, 1990), competition (Smith and Wall, 1997a,b) and habitat-type (Lane, 1975; Davies, 1990; Gregor, 1991). The myiasis habit may also be a consequence of the intense competition in carrion, resulting in some species having evolved the ability to occupy niches created by farmed livestock. The aim of this work was to investigate the abundance of the different species of the saprophagic blowfly community in three different habitats of south west England, to further define the role of habitat in their abundance and niche separation.

Materials and methods

Study sites

Two sites were sampled in this study. Site one was on an organic livestock farm in Failand, North Somerset, which is located in a rural area consisting mainly of pastureland for agricultural use and with little human activity. Site two was on a mixed farm in Long Ashton, North Somerset, located in a semi-rural zone less than 500m away from an area with housing and higher human activity. Each farm was situated approximately 5km from the city of Bristol and separated by 5km from each other. Both sites presented a variety of different patches of habitat within the farm, of which three were considered for this study: open field (grassland, with direct sunlight), hedgerow (mainly hawthorn and bramble, offering partial shade) and woodland (predominantly ash, hazel and birch, with complete shade).

Trapping

Modified bottle traps (Hwang and Turner, 2006) were used to catch blowfly specimens in good condition to allow identification. Each trap was baited with approximately 100g of fresh lamb liver. The liver was placed in a plastic container inside the trap and it was topped up with water during every collection to prevent bait desiccation. The bait was covered with a mesh and a rubber band to reduce oviposition.

On the 2nd of March 2016, five traps were distributed at least 20 m from each other in each habitat placed approximately 1.5 m off the ground and attached to a tree, for the woodland, or a fence post for the hedgerow. To sample in open habitats, pre-existing posts supporting wire fences with no associated hedge vegetation were used or, if unavailable, wooden posts were erected for the study prior to trapping. Fifteen traps were placed at each farm, five in each habitat with a total of 30 traps for both farms. The last collection and trap removal took place on the 5th of August 2016.

Collections were made every 3-6 days. At each collection, the upper part of the trap containing the flies was removed and replaced by a clean one for further trapping. Traps were taken back to the laboratory at the University of Bristol and placed at -20 °C for 20 min. Traps were then emptied and specimens were removed for further identification. Baits were replaced every 4-5 weeks; previous research has shown that the age of the baits has little effect on the blowfly catch size once past the initial stages of decomposition (Fisher et al., 1998). Once trapped flies had been removed,

calliphorids were separated from non-target species and identification was made under a dissecting microscope model Leica S6E using keys (Emden, 1954). The number of each species was recorded in relation to habitat and site.

Data analysis

The number of flies caught per trap per day was calculated by dividing the number of flies caught per trap (for each species) by number of days of trap operation since the last collections. Catch per day was used to remove any effect of the differences in time interval between collections. For each collection interval, mean temperature was calculated from the data recorded by a local weather station at Horfield/Filton, situated approximately 13 km from both farms. Due to the non-normal distribution of the count data for the calliphorid species collected here and the large proportion of zero counts, a generalised linear mixed model with a negative binomial error was selected for each species separately with the function `glm.nb` using RSTUDIO 3.4.2 (2015), where the influence of site (rural, semirural), habitat (open, hedge, woods) and temperature were included as fixed factors and the transformed fly count number (described above) as the dependant variable. Previous studies have shown that for overdispersed count data, negative binomial distribution models can provide better understanding of the probability distribution of different species (Sileshi, 2006). The best fit model was selected for each separate species based on the Akaike information criterion (AIC). If any, interactions between site and habitat were also analysed.

Results

A total of 17,246 calliphorid specimens were caught and identified. Of these 2,427 were *L. sericata*, 51 *L. richardsi*, 6,580 *L. caesar*, 307 *L. ampullacea*, 4,881 *Calliphora vicina* and 2,959 *C. vomitoria*. The study also found specimens of *L. silvarum* and *L. illustris*, however they were not included in the statistical analysis as the number of specimens caught for each was less than 10, this study did not recover any specimens of *L. bufonivora*.

Calliphorid species composition changed over the duration of the collection period (Fig1-5). *Calliphora vicina* and *C. vomitoria* were the first calliphorid species to emerge in the month of March when the average temperature was 6.8 °C. No *Lucilia* specimens were found in March. The two *Calliphora* species were also the most abundant calliphorids over the month of April; the average temperature reported for this month was 8.9 °C. In fact the highest catch recorded for the month of April of *C. vicina* was of 12 flies/trap/day. The first specimens of *L. sericata* and *L. caesar* were observed during late April at the semirural farm. The population of *C. vicina* decreased in the warmer months, June, July and August, while *Lucilia* populations increased over these months. The statistical

models showed that there was a significant effect of temperature on the number caught for all calliphorid species except for *C. vicina*, where temperature was not a significant factor (see supplementary data).

Of the 17,246 specimens, 7,876 flies were caught in the rural farm and 9,370 in the semi-rural farm. Site had a significant effect on the abundance of *L. sericata* ($z=7.142$, $P<0.001$; Fig 1) and *L. ampullacea* ($z=-9.591$, $P<0.001$; Fig 2); however, this factor had no association with the abundance of *L. caesar*, *L. richardsi*, *C. vicina* or *C. vomitoria*. The sheep blowfly *Lucilia sericata* was significantly more abundant at the semi-rural farm than in the rural farm, in contrast *L. ampullacea* was significantly more abundant at the rural farm.

The factor ‘habitat’ had a significant effect on the fly catch for all the species collected. The calliphorid community in ‘open’ habitats was dominated by *L. sericata* (Fig 1), however *C. vicina* was also frequently present in this habitat, although not as frequently as in hedge and woodland habitats (Fig. 5). The low abundance species, *L. richardsi*, was also more frequently found in this habitat, it was rarely found in hedgerows and it was not found at all in woodland traps.

The most abundant species in hedgerow habitats were *L. caesar* (Fig 3) and *C. vicina*. Statistical analysis showed that the abundance of the latter species was not significantly different between woodland and hedgerow habitats ($z=-0.172$, $P=0.86$). In woodland habitats *L. caesar* (Fig 3) and *C. vomitoria* (Fig. 4) were the most abundant, both species were also found in hedgerows but at lower abundances. The highest abundance of the rare species *L. ampullacea* was in woodland habitats (Fig 2).

There was a significant interaction between habitat and site on the catch of *L. sericata*, *L. caesar*, *C. vicina* and *C. vomitoria*; *L. sericata* was more common in the hedgerow habitats of the semirural farm (Fig. 1) than those of the rural farm ($z=-7.142$, $P<0.001$). Similarly, even when *L. caesar* was more abundant in the woodland habitats, it was occasionally found in open habitats, and statistical analysis showed that this happened more frequently in the semirural farm, than in open habitat of the rural farm ($z=-4.508$, $P<0.001$). In contrast, *C. vicina*, which was generally more frequent in hedgerow and woodland habitats, was more abundant in the open habitats of the rural farm than those of the semirural farm ($z=4.22$, $P<0.001$).

Discussion

Carrion is an unpredictable and ephemeral resource and diversity within carrion breeding insect community is thought to be structured by intense resource competition with ecophysiological, behavioural or phenological differences allowing niche partitioning in space and time (Cruickshank and Wall, 2002). However, the interspecific ecological difference that facilitate coexistence within the blowfly community are not fully understood.

Differences in habitat use may have an important impact on their population dynamics, through its effects on the intensity of competition, predation or parasitism (Hanski *et al.*, 1994). Understanding patterns of habitat use is also important, because heterogeneity in distribution affects the variance in catch and thereby determines the spatial scale, method and intensity at which sampling must be carried out (Southwood, 1976). For insect pests, the pattern of habitat use and the spatial scale of aggregation with specific parts of the habitat has a critical influence on the efficacy of almost all control techniques and therefore on the nature, application practicalities and cost of any control procedure. An understanding of the factors that determine the relative abundance of *Lucilia* is also of particular practical interest since *L. sericata* and *L. caesar* are of economic importance in livestock myiasis (MacLeod, 1943; Wall *et al.*, 1992a,b; Hall and Wall, 1995).

The present work took place over a single year and, given the highly variable weather of the UK, climatic variation between years might be expected to result in differences in the abundance of the various species recorded. More extensive research over several years would be required to assess this possibility. However, the findings presented here correspond with previous studies on spatial and temporal distribution of calliphorid flies, giving confidence in the underlying robustness of the trends identified. For example, studies have shown that *Calliphora* species to be more abundant in cooler months relative to *Lucilia* species (Greco *et al.*, 2014; Zabala *et al.*, 2014). The minimum temperature below which the development of *C. vicina* ceases was reported to be 2 °C (Greenberg, 1991) and recent laboratory studies estimated a minimum developmental temperature of 1°C and a requirement of 4,700 accumulated degree hours for the development from the egg hatch to pupation (Donovan *et al.*, 2006). The reduction in the abundance of *Calliphora* species in the carrion community during the warmer months could possibly be affected also by the presence of other carrion breeding species with higher threshold temperature development, increasing competition for food resources. The lower threshold temperature for *L. sericata* development is 9 °C (Wall *et al.*, 1992) and mean temperatures above 9 °C were not achieved until late April in the year of the study. Hence, *Lucilia* adults were not present during March and most of April. When *L. sericata* were present, the species was significantly more abundant in open habitats and rarely seen in the woodland. The high abundance of *L. sericata* in open relative to other habitats has also been recorded previously (Gregor, 1991; Smith and Wall, 1997; Martínez-Sánchez *et al.*, 2000). This pattern of habitat use may be related to light intensity and previous studies have suggested that the behaviour (Smith *et al.*, 2002) and trap catch size (Woodridge *et al.*, 2007) of *L. sericata* are strongly affected by light intensity, although microclimatic temperature and humidity tolerances may also be important (Cruickshank and Wall, 2002). The data also support previous studies where it is suggested that *L. sericata* is a synanthropic species (Fischer, 2000; Hwang and Turner, 2006), as the number of specimens recorded for the rural farm was much lower than that

one recorded for the semirural farm, and in fact, during the whole experiment this number did not surpass the 0.8 flies/trap/day in the rural farm.

In the present study, *L. caesar* was the most abundant calliphorid species, collected mainly from shaded habitats. In western Scotland *L. caesar* was the second most abundant species of myiasis agent in sheep strikes and occurred at a significantly higher frequency than in more southerly latitudes (Morris and Titchener, 1994). While it has been suggested that this may be due to lower temperature and higher humidity requirements for *L. caesar* (Wall *et al.*, 1992) there is no firm understanding of why the involvement of *L. caesar* in ovine cutaneous myiasis is rare in England although it is very common as a carrion breeding species in woodland habitats. Similarly, *L. illustris* is reported as a common species involved in flystrike cases in Norway (Brinkmann, 1976) and as the dominant species of the carrion fly community in Finland (Hanski and Kuusela, 1977). However in England *L. illustris* has not been reported involved in flystrike (Wall *et al.*, 1992a) and, in fact, our data alongside previous studies suggest that it is a rare species in England (Smith and Wall, 1997); the reason why *L. illustris* is rarely involved in flystrike cases in the UK is still unknown and further work is required to study this phenomenon.

Most natural carcasses are situated in shaded habitats, as dying animals seek shelter (Blackith and Blackith, 1990) and this means that the food resource available to *L. sericata* is limited, as it has been reported as a relatively poor inter-specific competitor with other calliphorid species (Smith and Wall, 1997; Grassberger *et al.*, 2003; Keirallah *et al.*, 2007). This could have played an important role in niche partitioning, possibly forcing *Lucilia sericata* to migrate to food resources with fewer potential competitors, such as living hosts in open habitats. However, more studies need to be carried out to determine and understand the pathway of the parasitic behaviour within this genus.

MacLeod and Donnelly (1957) suggested that relatively persistent fly distributions within the vegetational mosaic might be delimited by habitat requirements. The data presented here suggest that differences in phenology and habitat use between *Calliphora* and *Lucilia* are likely to be mediated most strongly by differences in temperature tolerance, whereas difference within species of the genus *Lucilia* are likely to be mediated by differences in humidity and desiccation tolerance and light intensity, resulting in effective niche partitioning. Desiccation tolerance may have conferred a behavioural advantage for *L. sericata* over other blowfly species, allowing it to become a more common agent of livestock myiasis in open pasture.

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Figure Legends

Fig. 1. Spatial and temporal distribution and abundance of *L. sericata*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 2. Spatial and temporal distribution and abundance of *L. ampullacea*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 3. Spatial and temporal distribution and abundance of *L. caesar*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 4. Spatial and temporal distribution and abundance of *C. vomitoria*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 5. Spatial and temporal distribution and abundance of *C. vicina*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 1. Spatial and temporal distribution and abundance of *L. sericata*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 2. Spatial and temporal distribution and abundance of *L. ampullacea*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 3. Spatial and temporal distribution and abundance of *L. caesar*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 4. Spatial and temporal distribution and abundance of *C. vomitoria*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).

Fig. 5. Spatial and temporal distribution and abundance of *C. vicina*. Month of study is displayed on the horizontal axis, the vertical axis shows the number of flies/trap/day recorded for the different habitats (open, hedge and woods) at different sites: a) rural; b) semirural. The median flies/trap/day is displayed within boxes representing first and third quartiles. Whiskers show 95% confidence intervals with outliers (dots).