Bulletin of Entomological Research (2002) **92**, 153–158 DOI: 10.1079/BER2001149

Aggregation and habitat use by *Lucilia* blowflies (Diptera: Calliphoridae) in pasture

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Abstract

The spatial distribution of blowflies of the genus *Lucilia* within fields in south west England was examined in 1999 and 2000. Blowflies are economically important agents of sheep myiasis in the UK and understanding local aggregation is an essential step in the development of appropriate sampling and fly control regimes. Fifty, 20 × 20 cm, non-odour-baited, sticky traps were used to catch flies, at randomized, 10 × 10 m grid co-ordinates in fields of permanent pasture. Clear aggregations were evident in all *Lucilia* distributions. All values of the σ^2:mean ratio were greater than 1. The catches were shown to be highly aggregated using Morisita's index of aggregation. Generalized linear modelling of binary presence/absence catch data was used to relate aggregation to microclimate and habitat. Deletion testing was used to identify significant terms in the models. In general, *Lucilia* blowflies were predominantly caught around the edges, in warmer and more humid areas of the field. The relationship between microhabitat and the distribution of *Lucilia* collected in 1999 was used as predictive model to explain the catches made in two fields in 2000. This gave a highly significant fit in one field (P = 0.001) and a relationship which approached significance in the second (P = 0.08). However, these regressions suggest that the relationships between abundance and microhabitat are complex and that 'hot spots' of blowfly catches were not necessarily found in the most extreme microclimate conditions. Nevertheless, microhabitat features do give a relatively good guide to presence or absence of *Lucilia* in the trap catches, thereby providing important information about the most appropriate location of traps to maximize and standardize sampling and control regimes.

Introduction

The spatial distribution and dispersal of an insect species within its local environment may have an important impact on its population dynamics, through its effects on the intensity of competition, predation or parasitism (DeJong, 1979; Rothman & Darling, 1991; Hanski *et al.*, 1994). Understanding aggregation 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 degree of aggregation and its spatial scale 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.

The degree of aggregation may be associated with environmental conditions or habitat structure, mediated by simple kinetic behaviour or tactic responses to specific kairomone or pheromone cues. Aggregation may also vary with factors such as life-cycle stage, population density or time of year. For highly mobile organisms, aggregations may be labile and hence understanding the nature and causes of the patterns can be difficult.

The blowflies *Lucilia sericata* (Meigen) and, to a lesser extent, *Lucilia caesar* (Linnaeus) (Diptera: Calliphoridae) are important facultative ectoparasites of mammalian hosts,

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particularly sheep (Hall & Wall, 1995). Adult females lay batches of about 200 eggs at each oviposition, deposited in the sheep wool close to the skin. The subsequent feeding activity of the larvae at the skin surface rapidly promotes extensive tissue damage, resulting in the development of inflamed, abraded and ulcerated areas of skin with progressive alopecia. Infestation is known as blowfly strike. A survey of England and Wales showed that 81% of strikes were composed of pure cultures of *L. sericata* alone, 13% of mixed cultures of *L. sericata* and *L. caesar* and 6% by *L. caesar* alone (Wall *et al.*, 1992a). In the more northerly and westerly areas of Britain, *L. caesar* becomes of increasing importance; a survey in Scotland showed that *L. caesar* ocurred in pure cultures in 8% of strikes and mixed cultures with *L. sericata* in 31% (Morris & Titchener, 1997). In Norway, *L. caesar* was found to be the primary species in 27 cases of sheep myiasis (Brinkmann, 1976).

In contrast to the relative importance of these two species in sheep strike, individuals of *L. caesar* are generally several times more abundant than *L. sericata*, although local density varies widely (MacLeod & Donnelly, 1957; Wall *et al.*, 1992b). Previous studies have indicated that *Lucilia* populations occur in distinct aggregations, but have variously suggested that these aggregations may be persistent (MacLeod & Donnelly, 1962) or ephemeral (Wall *et al.*, 1992b) and associated with ecologically distinct units (MacLeod & Donnelly, 1957), such as vegetation or transient food abundance (Smith & Wall, 1997a,b). Understanding the aggregation of these species is of particular importance due to the development of commercial traps for blowfly control (e.g. Strikeout®, Agrisense BCS Ltd, Pontypridd, UK). The cost-effectiveness of traps may be enhanced by their appropriate placement to maximize catch.

The aim of this study was to undertake a detailed analysis of the spatial distribution of *Lucila* within pastures and to attempt to identify any possible causes for aggregations, such as associations with specific habitat types.

Materials and methods

Trials were carried out during 1999 and 2000 in an area of farmland in the Woodspring district of North Somerset in south west England. Flies were trapped from fields which were used as permanent pasture and either cut for silage or grazed intermittently by cattle or sheep. The fields used were edged by hedgerows, composed predominantly of hawthorn *Crataegus monogyna* Jacq. (Rosaceae).

In the first year of this study, 1999, a single 100 by 130 m field (field A) was used; use of a second field had to be abandoned when livestock were introduced during trapping. Sticky-traps were used to collect flies. These traps were constructed of 20 × 20 cm squares of corrugated polypropylene (Correx®, Correx Plastics Ltd, Gloucester, UK). The polypropylene squares were covered on one side with a 20 × 20 cm sheet of white, sticky flypaper (AgriSense BCS Ltd, Pontypridd, UK), which was attached by metal clips. The squares were pinned down horizontally at ground level, with metal pegs and covered by a pegged dome of chicken-wire (mesh width 3 cm) to exclude larger animals. The sticky-traps had no semiochemical bait. The field was divided into 10 × 10 m squares and random number tables were used to generate coordinates on the grid at which 50 traps were positioned. Traps were placed out at 09.00 h and collected at 16.00 h (British Summer Time) each day for 13 days during July and August 1999.

In 2000, two adjacent, approximately 2 ha, fields were used (fields B and C). The traps were essentially similar to those used in 1999, but each 20 × 20 cm sheet of white, sticky, fly-paper was attached to a square of aluminium (20 × 20 cm) which was in turn fixed horizontally on top of a wooden stake. The wooden stakes were pushed into the ground so that the aluminium sheets were approximately 30 cm above ground level. Chicken-wire domes were not used. Again the traps were not baited. Fifty traps were positioned at random coordinates on a 10 × 10 m grid in each field. The traps were deployed in fields B and C for 10 days, from the 14th to the 24th of August.

Trapping was carried out over relatively short, discrete time periods in three different fields, at a single point each year. This was because the numbers of traps used may have removed a sufficiently large proportion of the *Lucilia* population to have had a significant impact on the numbers emerging in the successive generations in that area, resulting in lower catches later in the year (Smith & Wall, 1998).

In both years, the sticky flypaper was replaced every two days. During the 7-h sample period all green-coloured Diptera were removed from the traps for identification in the laboratory. In 1999, *L. sericata* was identified to species while other *Lucilia* were simply combined into a single 'other' category. In 2000, all *Lucilia* were identified to species. Other flies were removed and discarded.

Over each trapping period, temperature and humidity data were collected at each trap position, on four occasions for field A, and on eight occasions for fields B and C, using a hand-held probe (HI-8564, Hanna Instruments Ltd, Leighton Buzzard, UK). Wind velocity was also measured in fields B and C, at the same times as the temperature and humidity were measured, using a portable digital anemometer (Labfacility Ltd, London, UK). It took approximately 60 min to make the recordings at all traps in each field and any time-dependent effects were minimized by randomizing the order in which traps were visited. The position of the traps in relation to the nearest hedgerow was noted. The habitat type for each trap was considered as the distance between the trap and the nearest hedgerow, and as a binary variable indicating whether the trap was further than (0) or less (1) than 10 m away from the nearest hedgerow.

Results

In 1999, 224 *Lucilia* were caught; 58 were *L. sericata* and 166 were 'other' *Lucilia*. In 2000, 881 *Lucilia* were caught, only ten were *L. sericata*, 835 were *L. caesar*, 32 *L. illustris* (Meigen), three *L. ampulacea* Villeneuve, two *L. silvarum* (Meigen) and one *L. richardsi* Collin. For the data collected in 1999, the numbers of all *Lucilia*, *L. sericata* and all *Lucilia* excluding *L. sericata* were analysed separately. For the data collected in 2000, the numbers of *L. caesar* alone or the numbers of all *Lucilia* caught, were used in the analyses.

Blowfly aggregation

To create a three-dimensional plot, the total catch in each 10 × 10 m square over each sample period was first linearly interpolated so that every grid square was assigned a catch value. The interpolated data were then used to plot a greyscale image. This graphical representation indicates visually that aggregations of *L. sericata* (fig. 1a) and of other *Lucilia* excluding *L. sericata* are evident in field A in 1999 (fig.

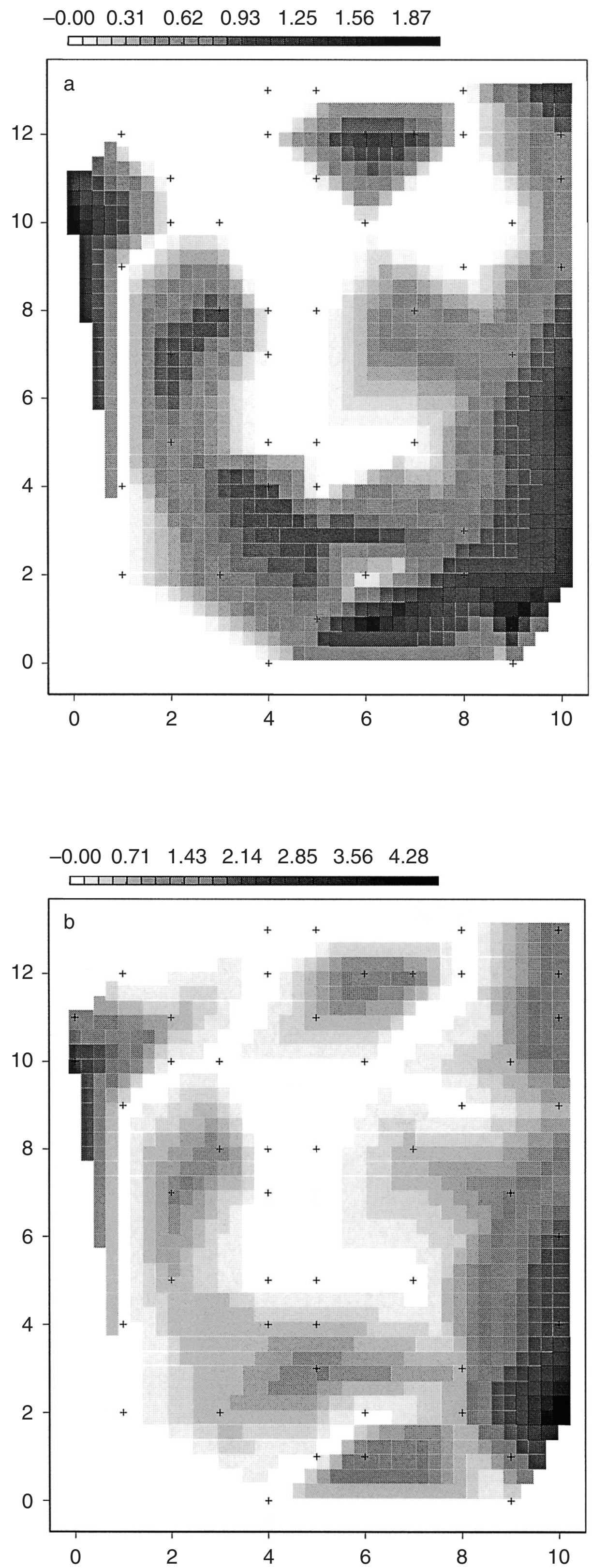

Fig. 1. Image maps of field A in 1999, showing data for linearly interpolated (a) log catch (+1) of the blowfly *Lucilia sericata*, (b) log catch (+1) of other *Lucilia* spp. Crosses show the positions of traps.

1b) and for *L. caesar* in fields B (fig. 2a) and C (fig. 2b) in 2000. Similar aggregations are evident in the pooled sample of all *Lucilia* caught in both years (data not shown).

To quantify this pattern, an index of departure from the Poisson distribution (D_p), as described by Hurlbert (1990), was used to test whether the blowfly distributions were random or not. The σ^2 to mean ratio was calculated as a measure of distribution (Southwood, 1976). The Morisita index (I_m) (Morisita, 1959) which calculates the likelihood that two randomly chosen individuals would be collected from the same trap, was used as an index of dispersion.

All values of the σ^2:mean ratio are greater than 1, suggesting a clumped distribution (table 1). The values of D_p for each data set are greater than 0.5, with the values for *L. caesar* in fields B and C very close to 1, which suggest that the blowfly distributions show a large departure from the Poisson distribution (table 1). The I_m values also show that the chance of a blowfly being caught in the same trap as another is much greater than would be expected from a random distribution of blowflies in all fields, again indicating clumped distributions in all fields (table 1). A χ^2 test shows that, in field A, the distribution of *L. sericata* was not significantly different from a negative binomial distribution (F = 0.54, df = 4). Although too few *L. sericata* were caught in any field in the 2000 trial for the data to be analysed, none of the ten *L. sericata* caught were found more than 10 m from a hedgerow.

Habitat use

Blowfly catches were transformed into binary presence/absence data. This resulted in catch data with a binomial error distribution. This permitted the catch data to be analysed with a generalized linear models (S-plus 2000, MathSoft Inc.) of the binomial family with a logit link function, in terms of the microclimate and habitat data (Venables, 1994). Deletion testing was used to identify significant terms of the models. The temperature, humidity and wind speeds recorded over each traping period were averaged for each trap prior to analysis. Where possible, the distance between the trap and the nearest hedgerow was used as the habitat variable, but in field C, where there were catches at few traps, the binary hedgerow/open field data sets were used.

For *L. sericata* in field A, there is a significant effect of the interaction between temperature and distance from the field edge on catch ($\chi^2 = 5.7$, $P = 0.016$). This is supported by fig. 1a, which shows that *L. sericata* were predominantly caught around the edges. For the other *Lucilia* in field A, there is a significant interactive effect of distance from hedgerow, temperature and humidity on catch ($\chi^2 = 6.7$, $P = 0.009$), with flies caught where the field was warmer and more humid.

In 2000, for *L. caesar* in field B, the predicted minimal model is an interaction between distance from hedgerow and mean temperature ($\chi^2 = 4.04$, $P = 0.04$) and an interaction between distance from hedgerow and mean wind velocity ($\chi^2 = 3.96$, $P = 0.05$); *L. caesar* were caught mainly in areas which were near hedgerows, in warmer areas and in areas where the wind velocity was lower. The minimal model predicted for *L. caesar* in field C in 2000 is an effect of distance ($\chi^2 = 11.5$, $P = 0.001$), mean temperature ($\chi^2 = 7.9$, $P = 0.005$) and mean relative humidity ($\chi^2 = 7.2$, $P = 0.007$), but not the interaction between them, with *L. caesar* again caught

https://doi.org/10.1079/BER2001149 Published online by Cambridge University Press

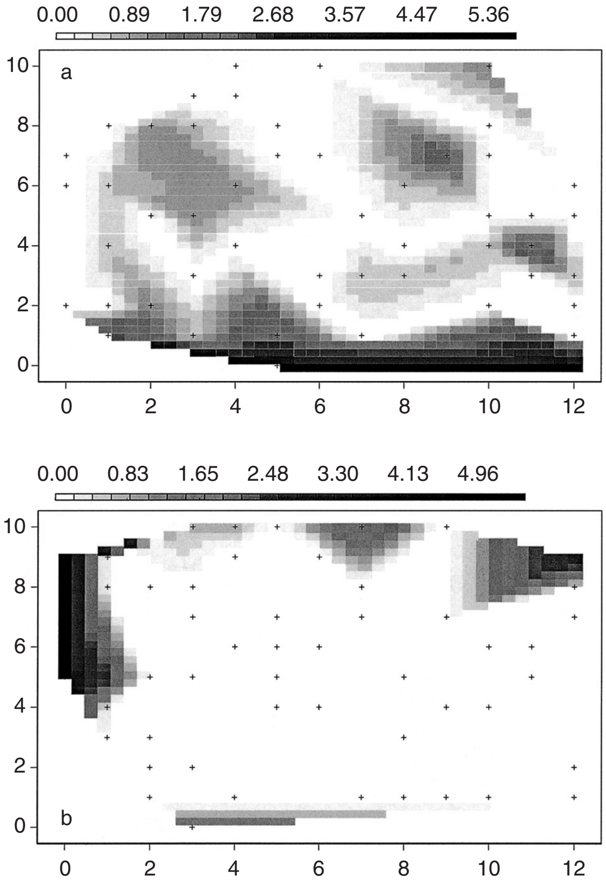

Fig. 2. Image maps showing data for linearly interpolated log catch (+1) of the blowfly *Lucilia caesar* in 2000 for (a) field B and (b) field C. Crosses show the positions of traps.

around field edges near hedgerows and in the warmer and more humid areas of the field.

Distribution prediction

To consider whether the observations of blowfly distribution might have practical application, for example in indicating the most appropriate location for the citing of monitoring traps, the GLM analysis was carried out again, using all the *Lucilia* caught in 1999. The minimal model (table 2), incorporating the interaction between distance, hedgerow, mean temperature and humidity was used to predict the distribution of *Lucilia* that would have been expected in 2000 in fields B and C. Regression of the number of all *Lucilia* caught in 2000, on each trap in each 10 × 10 m grid square, against the number predicted in that grid square by the fitted minimal model, shows that there is a significant relationship in the case of field C but not field B (fig. 3). Although the regression relationships are relatively weak, there does appear to be a useful correlation between the predicted presence or absence of *Lucilia* and their observed ocurrence.

Discussion

An understanding of the factors that determine the relative abundance of *Lucilia* is of intrinsic ecological interest. This is of particular practical significance for *L. sericata* and *L. caesar* because of the economic importance of livestock myiasis affected by these species (MacLeod, 1943; Hall & Wall, 1995). A number of previous trapping studies have suggested that *L. sericata* occurs in aggregations (MacLeod & Donnelly, 1957, 1962; Wall *et al.*, 1992b). MacLeod & Donnelly suggested in 1957 that relatively persistent fly distributions within the vegetational mosaic might be delimited by habitat preferences, although the same authors in 1962 argued that they could find no environmental differences to account for population peaks and that aggregations occurred within blocks of similar vegetation. In contrast, Wall *et al*. (1992b) suggested that *L. sericata* were aggregated throughout the season but that the location of the aggregations were not associated with vegetation type but varied in location over time. They suggested that since saprophytic or parasitic blowflies utilize discrete, ephemeral and spatially rare resources, the abundance of adult flies might be expected to mirror that of the larval resource. Hence, aggregations might be composed of cohorts of flies originating from one or more egg batches oviposited on carrion or a host animal simultaneously. As a result of the similar day-degree requirements for development of individuals from a single egg mass, flushes of adult emergence may occur in relatively localized areas resulting in temporary local population concentrations. Similarly, aggregations may be the result of the responses of adults to the presence of carrion, faeces or other protein sources required for maturation of eggs or oviposition.

It is notable that, with the exception of *L. caesar*, most species of British *Lucilia* occur at relatively low densities and are difficult to catch with unbaited traps. Hence, one of the major difficulties faced by this study was that in 1999, 50 traps caught only 224 specimens over 13 days and in 2000, 100 traps caught only 881 *Lucilia* over a period of 10 days. In the first year of the study, *L. sericata* made up 25% of the catch, but only 1.1% in 2000. The reason for the differences in catch composition observed between years in the present

Table 1. Total catch and indices of distribution and aggregation for *Lucilia* blowflies collected in three fields in 1999 (A) and 2000 (B and C). Also the average temperature (°C) and relative humidity (%) recordings (±s.d.) during the sampling periods.

Field	Catch	Total catch	σ^2 /mean	D_p	I_m	Temperature °C		Relative humidity (%)	
						Mean	s.d.	Mean	s.d.
A	*L. sericata*	58	2.19	0.61	2.07	22.9	6.98	70.9	12.9
	Lucilia spp.	166	44.5	0.62	14.2				
B	*L. caesar*	492	204.1	0.92	21.2	21.3	1.41	65.9	6.66
C	*L. caesar*	343	133.8	0.95	20.4	20.8	1.49	65.8	6.72

Table 2. Terms in the minimal generalized linear model (GLM), of the binomial family with the logit link function, for all *Lucilia* collected in 1999.

Term	df	Deviance	Residual df	Residual deviance	coefficient	*P*
Null			49	68.6	243.6	
Distance	1	5.18	48	63.4	–21.93	0.02
Temperature	1	0.03	47	63.4	–11.75	0.86
Humidity	1	1.24	46	62.1	–3.84	0.26
Distance : temperature	1	1.42	45	60.7	0.991	0.23
Distance : humidity	1	3.90	44	56.8	0.333	0.05
Temperature : humidity	1	0.75	43	56.0	0.184	0.38
Distance : temperature : humidity	1	6.70	42	49.3	–0.015	0.01

Distance is the distance between the trap and the nearest hedgerow. Temperature is the mean temperature (°C) at the trap position. Humidity is the mean per cent relative humidity at each trap position.

study is unknown but, as a result of these low numbers, it was essential to combine species to allow appropriate data analysis. Previous studies have recorded similar proportions of *L. sericata* to *L. caesar* and other *Lucilia* species (MacLeod & Donnelly, 1957; Wall *et al*., 1992a).

All previous studies of blowfly aggregation have used traps baited with carrion. This is likely to have artificially distorted the pattern by increasing the level of aggregation observed. The present study used unbaited sticky traps. Within fields, *Lucilia* appeared to be absent from large areas, present in small numbers in some areas, and relatively more abundant in other areas, creating 'hot spots'. The blowfly clusters appeared to be strongly associated with field edges and hedgerows. Hedgerows provide a more complicated architecture than open pasture, and may be used as roosts, areas to shelter and as cover from predators.

In this study, it has been assumed that, since the traps were unbaited and at least 10 m apart, the catches at each trap were independent of each other. It is however possible, that to some degree, one trap may have depleted the *Lucilia* population locally, lowering the catch at neighbouring traps. The occurrence or likely influence of such an effect on the observed relationship between microclimate, habitat, and fly distribution can not be assessed from the present study.

Smith & Wall (1997a,b) found that, when carrion and carrion baited traps were placed in different habitats around a field, significantly more *L. sericata* emerged from the carrion and were trapped, when the baits and carrion were located in the open centre of the field as opposed to under hedgerows or within woodland. They therefore suggested that *L. sericata* was predominantly an open habitat species. This conclusion is further refined by the results of the present study which suggest that, in the absence of odours, *L. sericata* aggregate near to the hedgerow at the edges of fields; they probably then move to open areas in the centre of the field to exploit resources when available, as shown by Smith & Wall (1997a,b). However, carrion bait positioned directly within hedgerow or nearby woodland evokes a relatively weak response from *L. sericata*, despite their proximity to this habitat, as shown in the present study. Hence, the response to odour cues is evidently modified by the habitat in which the cues are present. It is clearly important, therefore, that the spatial distribution of blowflies is monitored without the use of semiochemical attractants that work over long distances, since this is likely to influence blowfly distribution.

The ambient temperature around the traps was correlated with the distribution of blowflies in every field in this study. Blowflies are more active at higher temperatures

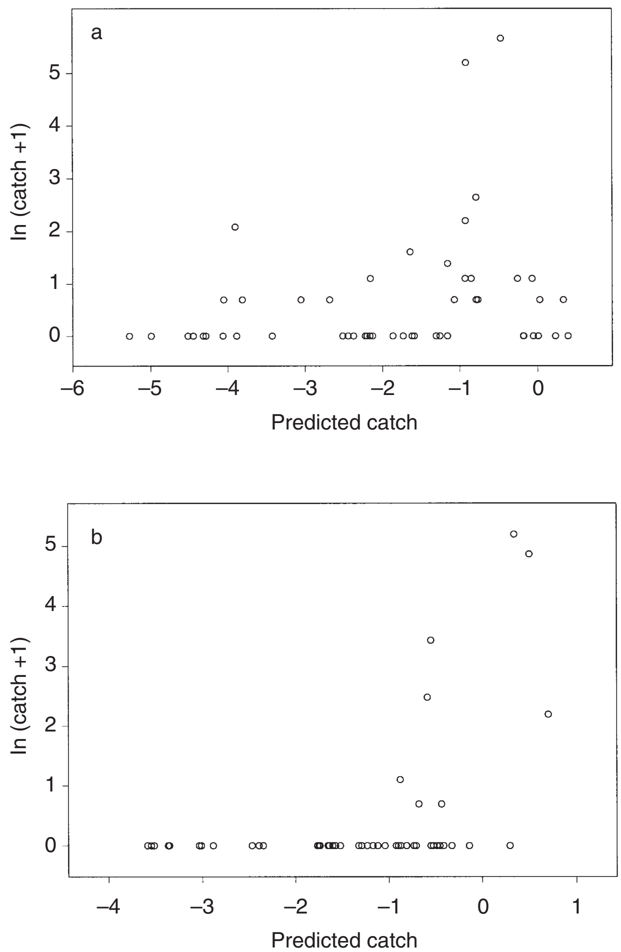

Fig. 3. Observed log number of all *Lucilia* caught in 2000 in each 10 × 10 m grid square, plotted against the number predicted in that grid square, on the basis of the GLM fitted to the data collected for all *Lucilia* in 1999; (a) field B, $R^2 = 0.06$, $F_{1,48} = 3.062$, $P = 0.08$; (b) field C, $R^2 = 0.20$, $F_{1,48} = 12.04$, $P = 0.001$).

(Wall & Smith, 1997) and active blowflies are more likely to be caught by the traps used. Humidity and wind velocity at the traps also had effects on the distribution of blowflies, but these effects were not apparent consistently in all of the fields. Wind speed is highly variable and is difficult to measure accurately in the field. It is probable, therefore, that the absence of a more consistent effect of wind speed in the present study may have been, at least in part, a result of the inadequacy of the way it was recorded.

Although the data were collected over 13 and 10 days in 1999 and 2000, respectively. It was not possible to consider the trap catches as time-series. In 1999 the fly numbers were simply too small to analyse day-by-day. In 2000, in fields B and C, 86% and 97% of the flies trapped, respectively, were collected in just three of the 10 days sampled. This probably reflects the relatively synchronized emergence patterns of these flies in the field (Hayes *et al.*, 1999).

When the relationship between habitat factors and the distribution of all *Lucilia* collected in 1999, was used as predictive model to explain the catches made in in 2000, a highly significant fit was obtained in one field (field C, $P = 0.001$) and a relationship which approached significance was obtained in the second (field B, $P = 0.08$). Hence, although local blowfly aggregations were significantly higher close to the field edge and in areas that were relatively warm and humid, these regressions suggest that clearly there are no simple linear relationships between abundance and habitat features and the 'hot spots' of blowfly catches were not found in the most extreme microclimate conditions. The analysis that was carried out used binary fly presence/absence data for each trap, which resulted in some loss of information and precision; the logistic regression model then gives predictions that are not binary, which makes interpretation problematic. Nevertheless, although the continuous relationships between observed and expected abundance are weak, the regressions do give a relatively good guide to presence or absence of *Lucilia* in the trap catches, thereby providing important information about the most appropriate location of traps to maximize and standardize sampling and control regimes.

Acknowledgements

The financial support of the Natural Environment Research Council (NERC grant GR3/11702) and the Royal Society are gratefully acknowledged. We would like to thank Kieren Pitts, Jenni Kakkonen, Russell Lisk, Amy Sanders and Christine Singfield for assistance with field work, Steve Paterson for advice with statistics and Katie Smith for assisting with fly identification.

References

Brinkmann, A. (1976) Blowfly myiasis of sheep in Norway. *Norwegian Journal of Zoology* 24, 325–330.

DeJong, G. (1979) The influence of the distribution of juveniles over patches of food on the dynamics of a population. *Netherlands Journal of Zoology* **29**, 33– 51.

Hall, M.J.R. & Wall, R. (1995) Myiasis in humans and domestic animals. *Advances in Parasitology* **35**, 258–334.

Hanski, I., Kuussaari, M. & Nieminen, M. (1994) Metapopulation structure and migration in the butterfly *Melitaea cinxia*. *Ecology* **75**, 747– 762.

Hayes, E., Wall, R. & Smith, K.E. (1999) Mortality rate, reproductive output and trap response bias in populations of the blowfly *Lucilia sericata*. *Ecological Entomology* **24**, 300–307.

Hurlbert, S.H. (1990) Spatial distribution of the mountain unicorn. *Oikos* **58**, 257–271.

MacLeod, J. (1943) A survey of British sheep blowflies. *Bulletin of Entomological Research* **34**, 65–88.

MacLeod, J. & Donnelly, J. (1957) Some ecological relationships of natural populations of calliphorine blowflies. *Journal of Animal Ecology* **26**, 1315–170.

MacLeod, J. & Donnelly, J. (1962) Microgeographic aggregations in blowfly populations. *Journal of Animal Ecology* **31**, 525–544.

Morisita, M. (1959) Measuring of the dispersion of individuals and analysis of the distributional patterns. *Memoirs of the Faculty of Science, Kyushu University Series F (Biology)* **2**, 215–235.

Morris, O.S. & Titchener, R.N. (1997) Blowfly species composition in sheep myiasis in Scotland. *Medical and Veterinary Entomology* **11**, 253–256

Rothman, L.D. & Darling, D.C. (1991) Spatial density dependence – effects of scale, host spatial pattern and parasitoid reproductive strategy. *Oikos*, **62**, 221–230.

Smith, K.E. & Wall, R. (1997a) The use of carrion as breeding sites by the blowfly *Lucilia sericata* and other Calliphoridae. *Medical and Veterinary Entomology* **11**, 38–44.

Smith, K.E. & Wall, R. (1997b) Asymmetric competition between larvae of the blowflies *Calliphora vicina* and *Lucilia sericata* in carrion. *Ecological Entomology* **22**, 468–474.

Smith, K.E. & Wall, R. (1998) Suppression of a population of the blowfly *Lucilia sericata* in sheep pastures using baited targets. *Medical and Veterinary Entomology* **12**, 101–108.

Southwood, T.R.E. (1976) *Ecological methods*, 2nd edn. Cambridge University Press.

Wall, R., French, N.P. & Morgan, K. (1992a) Blowfly species composition in sheep myiasis in Britain. *Medical and Veterinary Entomology* **6**, 177–178.

Wall, R., Green, C.H., French, N.P. & Morgan, K.L. (1992b) Development of an attractive target for the sheep blowfly *Lucilia sericata*. *Medical and Veterinary Entomology* **6**, 67–74.

Wall, R. & Smith, K.E. (1997) The potential for control of the blowfly *Lucilia sericata* using odour-baited targets. *Medical and Veterinary Entomology* **11**, 335–341.

Venables, W.N. (1994) *Modern applied statistics with S-Plus*. New York, Springer.

(Accepted 29 November 2001)