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Predicting calyptrate fly populations from the weather, and probable consequences of climate change

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Summary

1. Calyptrate flies include numerous species that are disease vectors and have a high nuisance value, notably *Musca domestica*. Populations are often associated with livestock farms and domestic waste disposal facilities such as landfill, where the accumulating organic matter provides suitable breeding conditions for a range of species.

2. We examined the relationship between fly numbers and weather conditions using a 4-year data set of weekly fly catches from six sites in southern UK, together with meteorological data. The first 3 years were used to develop predictive models, and these were then used to forecast fly populations in the fourth year. The accuracy of these predictions was assessed by comparison with the actual fly catches for that year. Separate models were developed for *M. domestica*, *Calliphora* spp. and all calyptrate flies combined.

3. Predictions based only on humidity, temperature and rainfall were strongly correlated with observed data (r^2 values ranged from 0·52 to 0·84), suggesting that fly population changes are largely driven by the weather rather than by biotic factors. We can forecast fly populations so that control measures need only be deployed when weather conditions are suitable for a fly outbreak, reducing the need for prophylactic insecticide use.

4. Climate change was simulated using the most recent predictions of future temperature increases. Our models predicted substantial increases in fly populations up to 244% by 2080 compared with current levels, with the greatest increases occurring in the summer months.

5. *Synthesis and applications.* Models developed use weather data to predict populations of pestiferous flies such as *M. domestica*, which may prove valuable in integrated control programmes. These models predict substantial increases in fly populations in the future under likely scenarios of climate change. If this occurs we may expect considerable increases in the incidence of fly-borne disease.

Key-words: *Calliphora*, disease transmission, human waste, humidity, *Musca domestica*, temperature

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Introduction

It is now widely accepted that the climate is changing as a result of 'greenhouse gases' produced by human activity. Predictions for warming vary, but most range from 1·5 °C to 5 °C by 2080 (Hulme *et al.* 2002). Changes to precipitation patterns are also likely, but are more difficult to predict with accuracy, although most models suggest that winter rainfall will increase in northern temperate regions (Houghton *et al.* 1996; Hulme *et al.* 2002). These changes are expected to have profound effects on species richness; recent studies predict that up to 37% of organisms may be 'committed to extinction' by 2050 because of climate change (Thomas *et al.* 2004). Major consequences for agricultural production (Parry 1992; Rosenzweig & Hillel 1998; Kriticos *et al.* 2003), forestry (Schwartz 1992), plant community composition (Buckland *et al.* 2001), the incidence of insect pest outbreaks (Sutherst 1995; Cannon 1998;

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Tenow *et al*. 1999) and of diseases transmitted by insects (Langford & Bentham 1995; Lindsay & Birley 1996; Sutherst 1998) are also expected. Attention has focused particularly on butterflies and birds, two groups for which extensive distributional and abundance data are available. For both groups specialized, sedentary species and those with a narrow latitudinal range appear to be most at risk of extinction as the climate warms (Roy *et al*. 2001; Bryant, Thomas & Bale 2002; Crick 2004; Julliard, Jiguet & Couvet 2004; Thomas *et al*. 2004). However, vagile generalists with broad latitudinal tolerance are likely to cope better, and thermophilic species (including many insect pests) may increase in abundance (Sutherst 1995; Cannon 1998; Baker *et al*. 2000).

Many calyptrate flies (Diptera: Cyclorrhapha: Calyptratae), particularly species of the Muscidae, are thermophilic, vagile and have large latitudinal ranges (Crosskey & Lane 1993). The propensity of the adults of many species to feed on human food, as well as refuse and excrement, means that they are important vectors of human disease (Crosskey & Lane 1993). Some calyptrates also cause myiasis in humans and livestock (Hall & Smith 1993), and are intermediate hosts of parasitic nematodes attacking livestock (Snow 1974). The annoyance and public health risks associated with large populations of such flies are thus considerable, and potential increases in their abundance as a result of climate change are a cause for concern.

Human populations produce considerable quantities of waste, with a large organic component suitable as a breeding site for many calyptrate fly species (Schoof, Mail & Savage 1954; Siverly & Schoof 1955a,b; Wilton 1961; Ikeda *et al*. 1972; Dirlbek 1986; Ferriera & Lacerda 1993; Werner 1997). Up to 10 million flies can emerge from just 1 ha of household waste (Abdel-Gawaad & Stein 1978). In Japan, Imai (1985) found that 1300–1500 flies emerged m^{-2} of landfill surface in 1 month following deposition. The abundance of food provided by the regular supply of organic waste, combined with above-ambient temperatures present immediately below the surface layers, helps promote the rapid proliferation of many fly populations throughout much of the year (Goulson, Hughes & Chapman 1999; Howard 2001). Species that are particularly likely to be problematic in terms of human health include the housefly *Musca domestica* Linnaeus (Muscidae) and bluebottles (*Calliphora* spp., Calliphoridae). These are synanthropic species, living in close association with humans. *Musca* larvae will develop in a wide range of decomposing organic material, while those of *Calliphora* feed primarily on animal matter (Colyer & Hammond 1968). However, there are many other species of pestiferous medium to large flies that breed within the organic component of human waste (Dirlbek 1986; Ferriera & Lacerda 1993).

A notable feature of fly populations, particularly those of *M. domestica*, is their propensity for very rapid fluctuations in population density, often with adult numbers increasing by up to two orders of magnitude in a few days (Imai 1984; Essa & El Sibae 1993; Goulson, Hughes & Chapman 1999). These population outbreaks are a major cause for concern because high density populations have a high nuisance value and may cause local outbreaks of disease such as gastro-enteritis.

We used a 4-year data set of weekly fly records from southern England to examine whether numbers of *M. domestica*, *Calliphora* spp. and all calyptrate flies can be predicted from meteorological data. We use models derived from this data set to predict numbers of flies under the warmer climatic conditions that may be expected in the future.

Materials and methods

DATA COLLECTION

Fly populations were monitored using 40 × 24·5-cm yellow sticky traps (Agrisense-BCS Ltd, Pontypridd, UK), a standard technique for studying fly distribution and abundance (Black & Krafsur 1985; Hogsette, Jacobs & Miller 1993; Goulson, Hughes & Chapman 1999). These traps were hung at approximately 1–1·5 m above ground level at six sites in southern England, UK (Table 1). Forty-six traps $week^{-1}$ were deployed between 1 January 2000–31 December 2003 (9568 traps in total). Three of the six trapping sites were immediately adjacent to active landfill sites, these being areas where flies are often particularly numerous. The landfill sites were subjected to regular insecticidal spraying in the summer months.

The flies caught were initially categorized into the following taxonomic groupings: *M. domestica*, *Musca*

Table 1. Locations of fly monitoring traps, with UK national grid reference, brief site description and mean catch of all pestiferous flies per trap per week over 4 years

Site	No. traps	Grid reference	Site description	Mean numbers of flies per trap per week ± SE
Paulsgrove landfill	8	SU 643 045	Perimeter of landfill site	8·78 ± 0·42
Paulsgrove	4	SU 642 048	Scrub 100–200 m from landfill	9·90 ± 0·41
Port Solent	12	SU 641 048	Coastal urban 500–700 m from landfill	4·52 ± 0·22
Gosport	4	SZ 605 987	Coastal urban	3·64 ± 0·19
Lymington	8	SU 315 935	Perimeter of landfill site	34·6 ± 2·78
Ringwood	10	SU 125 065	Perimeter of landfill site	18·1 ± 0·85

autumnalis Degeer, *Calliphora* spp., *Fannia* sp., *Lucilia* spp., *Pollenia* spp., *Sarcophaga* spp. and other calyptrate Diptera. However, only *M. domestica* and *Calliphora* spp. were sufficiently abundant for meaningful analysis. Meteorological data were obtained from the Meteorological Office (Exeter, UK) for a station in Southampton (national grid reference SU 427 105) that was sited approximately equidistant, at a distance of 15–20 km, between the various trapping sites. The distance between the site for collection of meteorological data and those used for fly trapping was a source of error but was unavoidable because meteorological stations were not present close to each of the trapping sites. It was judged that weather was unlikely to vary greatly over this small geographical scale, particularly when using weekly means.

ANALYSES

Pearson product-moment correlation coefficients between the log of the mean catch per trap at each site were calculated to determine whether different populations fluctuated in approximate synchrony. Having established that this was the case (see the Results), mean catch per trap across all sites was used in the development of a predictive model. The rationale for this was to develop a model able to predict fly populations in southern UK, rather than models specific to individual sites.

The analysis of changes in fly numbers and the weather was based on a Gompertz model for log index (or first-order autoregressive scheme) with weather variables as covariates, following a protocol developed by Roy *et al.* (2001). For a simple model with two weather variables, the fly population in a particular week is given by:

$$P_{t+1} = a + b_0P_t + b_1W_1 + b_2W_2$$

where P_t is the fly population in week t, W_1, W_2 are the values of the weather variables, and a and b are constants. By including the effect of the fly population in the previous week we allowed for density-dependent effects.

Data for the first 3 years (2000–02) were used to build a predictive model. For *M. domestica*, *Calliphora* spp. and all calyptrate flies combined, mean catch per trap was calculated and transformed to log (catch + 1) before analysis. Because values used were means of 46 traps there were very few zero values, even in winter. Hourly values for temperature and humidity and daily values for rainfall were used to calculate weekly means for air temperature, rainfall (per day) and humidity. Means for each of the 4 weeks prior to trapping, and the overall mean for 2-, 3- and 4-week periods prior to trapping were included as potential covariates in the model (21 in total). The time period up to 4 weeks was chosen because this is sufficient to span the entire life-cycle of flies such as *M. domestica* during the warmer months (Crosskey & Lane 1993).

Following Roy *et al.* (2001), the 21 potential explanatory weather variables were initially screened by fitting each of them singly to the data for each of the three taxonomic groupings of flies (*M. domestica*, *Calliphora* spp. and all calyptrate flies). Quadratic effects of weather variables were also examined. Any variable that was statistically significant at the 10% level was retained for further consideration, thus reducing the chances of missing effects.

For each of the three fly groups, the selected set of weather variables was then analysed further by best subsets regression to find the best-fitting model (highest r^2). The Akaike information criterion with correction for small sample size was used to compare the fit of models containing different numbers of weather variables (Hurvich & Tsai 1989). The validity of best subsets regression can be questioned because a large number of potential models were examined, and the r^2 value of the best model was likely to be an overestimate of the true value. The weather variables used were also correlated with one another, which could lead to erroneous rejection of important explanatory variables. Thus it was essential to have an independent test of the validity of such models. We therefore tested the models by using them to predict fly populations for 2003, based on climatic data and using the observed fly density for the preceding week. This is an approach that could be taken if trying to predict fly numbers on a week-by-week basis as part of an integrated control programme. Predictive success was measured by regressing observed numbers against the predictions (Roy *et al.* 2001). A more stringent test proposed by Kleijnen, Bettonvil & Van Groenendaal (1998) was also used.

It might be useful to be able to predict future fly populations in situations where no quantitative data are available on previous or present fly numbers. To this end the above procedure was repeated excluding the autoregressive term (fly population size in the previous week).

To examine the likely effects of climate change on fly numbers, models were recalculated using the full 4-year data set. These models were then used to predict fly populations under elevated temperatures. Predictions for climatic temperature increases were taken from Hulme *et al.* (2002) and were specific for south-central England. We used their 'medium-low emission' and 'high emission' scenarios, which predict mean temperature increase per season. We used their predictions to modify the observed weather data for 2000–03, leaving humidity and rainfall unchanged but raising the average temperature by between 1 °C and 5 °C in each season (Table 7). Initial fly density was set at the observed level for the first week of the data set but then the predictions for the previous week were used subsequently so that each model was free-running for the 4-year period. The predicted population under these elevated temperature regimes was then compared with the observed populations in this 4-year period.

Results

In total 102 890 calyptrate flies were recorded, of which 19 914 were *M. domestica* and 6031 were *Calliphora*

Table 2. Species composition and abundance of synanthropic Diptera and a list of other abundant calyptrate species caught on sticky traps on landfill sites in southern England

Species	% of total catch	Mean catch per trap per week
Housefly (*Musca domestica*)	17·4	2·50
Bluebottle (*Calliphora vomitoria* + *Calliphora vicinia*)	9·00	1·29
Greenbottle (*Lucilia* spp.)	5·23	0·75
Face fly (*Musca autumnalis*)	0·3	0·04
Lesser housefly (*Fannia* spp.)	0·7	0·10
Flesh fly (*Sarcophaga* spp.)	1·9	0·27
Cluster fly (*Pollenia rudis* + *Pollenia amentaria*)	1·6	0·23
Other calyptrate Diptera	63·9	9·16
Phaonia spp.		
Polietes lardaria (Fabricius)		
Neomyia cyanella (Meigen)		
Mesembrina meridiana (Linnaeus)		
Graphomyia maculata (Scopoli)		
Scathophaga stercoraria Linnaeus		
Eustalomyia spp.		

Table 3. Pearson product–moment correlation coefficients between total pestiferous fly catches at different sites ($n = 199$). All are significant at $P < 0{\cdot}001$

	Paulsgrove landfill	Paulsgrove	Port Solent	Gosport	Lymington	Ringwood
Paulsgrove landfill	*					
Paulsgrove	0·640	*				
Port Solent	0·463	0·532	*			
Gosport	0·487	0·581	0·495	*		
Lymington	0·478	0·499	0·480	0·516	*	
Ringwood	0·522	0·512	0·543	0·503	0·587	*

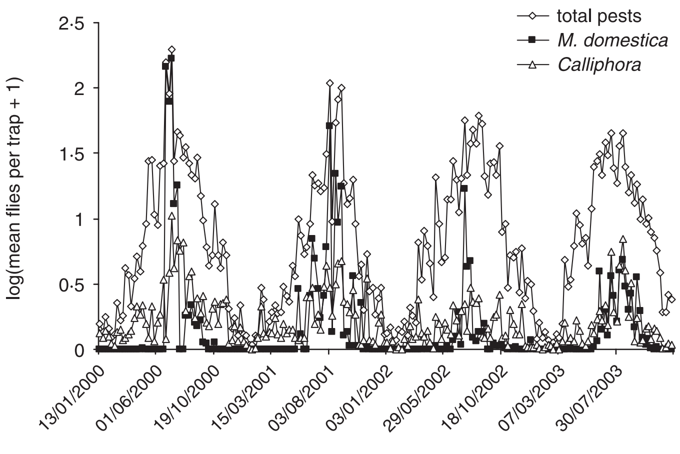

Fig. 1. Mean numbers of *M. domestica*, *Calliphora* spp. and total calyptrate flies caught per trap per week for the 4 years of trapping.

spp. A great many other calyptrate fly species were also captured, although most were relatively rare (Table 2). Numbers varied enormously with season (Fig. 1), with few flies caught between November and April and large numbers during the summer months. It was also noticeable that 2000 and 2001 had higher fly numbers in the summer than 2002 and 2003, with some very high peaks of up to 200 flies trap^{-1} (Fig. 1). These were in part attributable to the *M. domestica* population.

Populations of *M. domestica*, *Calliphora* spp. and all calyptrate flies combined were correlated in all pairwise comparisons between sites. Pearson product–moment correlation coefficients varied from 0·404 to 0·906 for *M. domestica*, from 0·451 to 0·852 for *Calliphora* spp. and from 0·463 to 0·640 for all calyptrate fly species ($P < 0{\cdot}001$ for all comparisons; Table 3). Traps positioned on the perimeter of active landfills were within 10 m of areas subjected to insecticidal sprays during the summer. However, comparisons between traps situated on the perimeter of the Paulsgrove landfill with those in scrubland 100–200 m distant, and in an urban area 500–700 m from the landfill, showed a close correlation in fly numbers (Table 4). Henceforth, all results are for mean catch per trap across all sites.

Table 4. Pearson product–moment correlation coefficients between fly catches at the Paulsgrove landfill and sites 100–200 m and 500–700 m distant from the landfill ($n = 199$)

		Correlation
100–200 m from landfill	*M. domestica*	0·778***
	Calliphora spp.	0·650***
	All calyptrate flies	0·640***
500–700 m from landfill	*M. domestica*	0·756***
	Calliphora spp.	0·661***
	All calyptrate flies	0·463***

***$P < 0{\cdot}001$.

Catches of all three fly groups were significantly positively correlated with catch in the previous week (Table 5). Weather variables also explained a significant proportion of the variation in numbers of all three fly groups examined during 2000–02 (Table 5). Although weather data for 4 weeks up to the fly trap collection were included in the analysis, the weather in the first of these 4 weeks had no significant effect in any of the three models. Temperature was the most powerful predictor for all three fly groups, with a generally positive correlation between fly catch and temperature in the 3 preceding weeks. For *M. domestica*, temperature in the week up to trap collection was the best single predictor, although other aspects of the temperature in the preceding 3 weeks independently contributed significant predictive power to the model. For *M. domestica*, neither rainfall nor humidity had any significant effects.

For *Calliphora* spp., numbers were best explained by the mean temperature in the preceding 3 weeks, and there was also an independent negative effect of rainfall in the period 2–3 weeks earlier. For all calyptrate flies combined, as with *M. domestica*, temperature in the week up to trap collection was the best single predictor, with both rainfall and humidity in this week having smaller negative effects.

The predicted populations for 2003 was closely correlated with the observed fly populations for all three fly groups (Fig. 2). Kleijnen *et al.* (1998) propose a more stringent test for predictive models of this type, in which the difference between observed and predicted values is regressed against the sum of their values. If the model is accurate there should be no significant relationship. For all pests combined and for *M. domestica* there was no significant relationship ($F_{1,46} = 2{\cdot}55$ and 0·014, respectively). However, the model for *Calliphora* failed this test ($F_{1,46} = 21{\cdot}5$, $P < 0{\cdot}001$): predictions tended to be slightly higher than observed values in 2003 (Fig. 2).

When models were reconstructed without incorporating previous fly population size, their predictive power was reduced but weather alone was found to provide significant predictive value (compare Table 5a and Table 5b). Once again temperature was the most powerful predictor for all three fly groups, with smaller negative effects of high humidity and rainfall (Table 5). Temperature had a generally positive effect on fly numbers, but for *M. domestica* there was also a significantly negative quadratic term for temperature in the period 1–2 weeks prior to capture, indicating that very high temperatures may have a delayed negative effect on numbers.

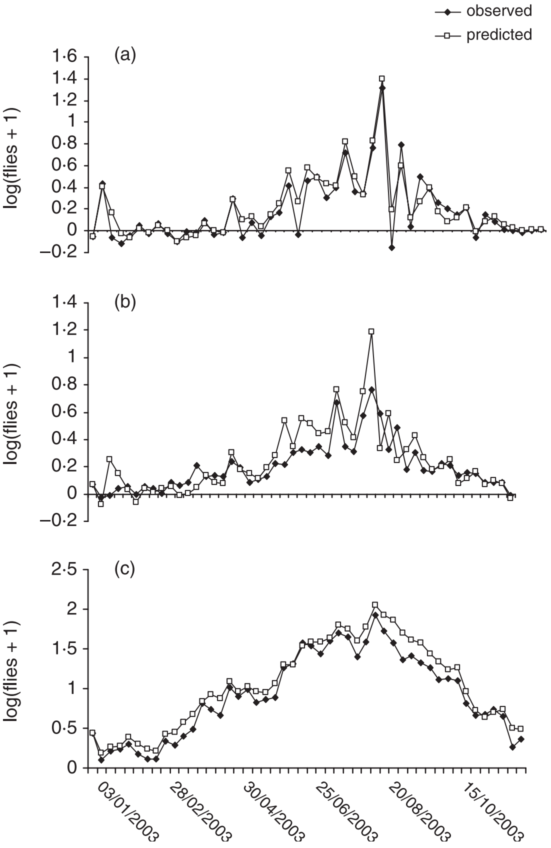

Fig. 2. Predicted and actual weekly catches during 2003. Predictions were produced by examining the relationship between fly numbers and weather variables in 2000–02, and then weather variables were used to predict fly numbers in 2003. Regression of observed vs. predicted numbers: $F_{1,48} = 343$, $P < 0{\cdot}001$, $r^2 = 0{\cdot}880$ for *M. domestica*; $F_{1,48} = 142$, $P < 0{\cdot}001$, $r^2 = 0{\cdot}751$ for *Calliphora* spp.; $F_{1,48} = 1853$, $P < 0{\cdot}001$, $r^2 = 0{\cdot}976$ for all calyptrate flies. (a) *Musca domestica*; (b) *Calliphora* spp.; (c) all calyptrate flies.

Models based on the full 4-year data set were broadly similar to those evaluated above (Table 5c). These were then used to predict the effects of climate change. For all three fly taxa, the predicted effects of climate change were an increase in abundance (Table 6). *Calliphora* spp. were least affected by climate change, with predicted increases of abundance of up to 85% by 2080 under the worst-case scenario (and it must be noted that the *Calliphora* model tended to over-estimate numbers). The models for *M. domestica* and for all flies combined (which did not overestimate numbers when tested against 2003 data) predicted dramatic increases (Table 6 and Fig. 3). For example *M. domestica* numbers were predicted to increase by 244% by 2080 under the worst-case climatic scenario, and by 156% under the moderately optimistic medium–low emissions scenario. Increases were most pronounced in the summer months (Fig. 3).

Table 5. Significant contributory factors explaining numbers of *M. domestica*, *Calliphora* spp. and all calyptrate flies during the first 3 (a, b) or all 4 (c) years of sampling. Unless otherwise stated, weather variables are weekly means. t, week up to trap collection; $t-1$, preceding week, etc. 'Fly count' refers to the mean catch per trap of the relevant fly taxa in the previous week. r^2 values indicate the proportion of the observed variation explained by the minimum adequate model shown. (a) Model includes fly count in previous week; (b) model without inclusion of fly count for previous week; (c) model with full data set to predict effects of climate change

(a)	*M. domestica*			*Calliphora* spp.			All calyptrate flies		
Covariate	$F_{(\text{d.f.}=1,142)}$	Parameter estimates ± SE	Partial r^2	$F_{(\text{d.f.}=1,144)}$	Parameter estimates ± SE	Partial r^2	$F_{(\text{d.f.}=1,144)}$	Parameter estimates ± SE	Partial r^2
Fly count$_{t-1}$	64·8***	0·555 ± 0·069	0·313	141***	0·708 ± 0·060	0·495	52·2***	0·482 ± 0·067	0·266
Temperature$_t$							41·9***	0·051 ± 0·008	0·225
(Temperature$_t$)^2	15·5***	0·012 ± 0·003	0·099						
Rain$_t$							4·2*	–0·012 ± 0·006	0·028
Humidity$_t$							4·59*	–0·007 ± 0·003	0·031
Rain$_{t-2}$				4·01*	–0·008 ± 0·04	0·027			
Temperature$_{t-1}$	5·33*	0·171 ± 0·074	0·036						
Temperature$_{t-2}$	8·05**	0·115 ± 0·040	0·054						
Temperature in previous 3 weeks	5·84*	–0·292 ± 0·121	0·039	6·32*	0·010 ± 0·004	0·042			
(Temperature in previous 2 weeks)^2	10·7**	–0·011 ± 0·003	0·070						
Intercept	0·027	–0·031 ± 0·188	–	0·069	–0·012 ±	–	2·55	0·436 ± 0·273	–
r^2	0·522			0·693			0·838		

(b)	*M. domestica*			*Calliphora* spp.			All calyptrate flies		
Covariate	$F_{(\text{d.f.}=1,144)}$	Parameter estimates ± SE	Partial r^2	$F_{(\text{d.f.}=1,149)}$	Parameter estimates ± SE	Partial r^2	$F_{(\text{d.f.}=1,140)}$	Parameter estimates ± SE	Partial r^2
Temperature$_t$	4·03*	–0·073 ± 0·036	0·027				324***	0·100 ± 0·006	0·699
(Temperature$_t$)^2				98·1***	0·002 ± 0·000	0·397			
Humidity$_t$							13·6***	–0·013 ± 0·004	0·088
Rain in previous 4 weeks							7·93**	–0·055 ± 0·020	0·054
Rain$_{t-3}$							5·04*	0·022 ± 0·010	0·035
(Rain$_{t-1}$)^2							4·32*	0·002 ± 0·001	0·030
(Temperature in previous 2 weeks)^2	14·1***	0·012 ± 0·003	0·089						
(Temperature$_{t-1}$)^2	13·2***	–0·007 ± 0·002	0·084						
(Humidity$_{t-2}$)^2	4·12*	0·001 ± 0·000	0·028						
Intercept	0·115	–0·096 ± 0·283	–	0·224	0·015 ± 0·032	–	7·35**	0·849 ± 0·313	–
Model r^2	0·315			0·397			0·776		

(c)	*M. domestica*			*Calliphora* spp.			All calyptrate flies		
Covariate	$F_{(\text{d.f.}=1,195)}$	Parameter estimates ± SE	Partial r^2	$F_{(\text{d.f.}=1,195)}$	Parameter estimates ± SE	Partial r^2	$F_{(\text{d.f.}=1,192)}$	Parameter estimates ± SE	Partial r^2
Fly count$_{t-1}$	78·4***	0·535 ± 0·060	0·287	178***	0·702 ± 0·053	0·477	114***	0·572 ± 0·054	0·372
Temperature$_t$							45·6***	0·042 ± 0·006	0·192
(Temperature$_t$)^2	18·0***	0·003 ± 0·001	0·085						
(Temperature in previous 2 weeks)^2	9·58**	–0·002 ± 0·01	0·047						
Temperature in previous 3 weeks				9·81**	0·010 ± 0·003	0·048			
Rain$_t$							7·22**	–0·013 ± 0·005	0·036
Intercept	2·88	–0·056 ± 0·033	–	1·78	–0·045 ± 0·034	–	4·62*	–0·110 ± 0·051	–
r^2	0·506			0·659			0·844		

*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$.

Table 6. Predicted increases in temperature assuming two alternative climate change scenarios from Hulme *et al*. (2002), and resulting predictions for changes in fly numbers. The 'medium–low emissions' scenario is moderately optimistic while that of 'high emissions' assumes that attempts to reduce emissions in the future are largely unsuccessful. Predicted fly numbers are expressed as a percentage increase compared to mean fly populations at observed temperatures in 2000–03 and are averages for the entire 4-year simulated period

	Medium–low emissions			High emissions		
	2020	2050	2080	2020	2050	2080
Predicted increase (°C)						
Winter	1	1·5	2	1	2	3·5
Spring	1	1·5	2·5	1	2	3·5
Summer	1·5	2·5	4	1·5	3·5	5
Autumn	1·5	2·5	3·5	1·5	3	5
M. domestica	45·7	84·3	156	45·7	128	244
Calliphora	22·1	36·7	59·3	22·1	50·5	85·3
Total pests	40	72·9	136	40	110	204

Discussion

Previous studies have suggested that one consequence of global climate change will be that some insect pests such as codling moth *Cydia pomonella*, Colorado beetle *Leptinotarsa decemlineata* and various aphid species will expand their ranges northwards and increase their abundance in parts of their current range (Cannon 1998; Rafoss & Saethre 2003) (although it must be noted that for herbivores there is no clear consensus as to the likely outcome of the complex interactions between climate change, CO_2 levels and plant–insect interactions, Newman 2004). A reduction in winter frosts is likely to play a key role in allowing northward advancement of some pest species (Bale 2002).

Our study demonstrates that calyptrate flies are likely to be among the species that respond positively to a warming climate: population fluctuations were strongly determined by the weather and we predict that small increases in temperature can lead to major increases in fly population density. Our most accurate model was for *M. domestica*, perhaps because this was the only taxonomic grouping used that consisted of a single species. Differential responses to weather of different species within the genus *Calliphora* and within the large group 'calyptrate flies' could lead to inaccuracies in the model. None the less, fly population size could be predicted with reasonable accuracy, despite predictive meteorological data having been obtained from a site some distance away from where the flies were caught.

Fly populations at all of the six monitoring sites were strongly correlated, suggesting that they fluctuate in approximate synchrony. This suggests that insecticidal sprays on landfill sites do not substantially alter the pattern of population fluctuations compared with neighbouring sites, although they may well reduce the overall population in the vicinity.

The key pest species associated with human waste is *M. domestica*, because it undergoes occasional and spectacular population outbreaks, and because of its propensity to enter human habitations (Imai 1984, 1985; Essa & El Sibae 1993). It is usual for waste disposal sites such as landfills to be sprayed prophylactically with synthetic insecticides (Imai 1985), but this is neither satisfactory nor particularly effective because it poses a health risk to humans and houseflies often exhibit cross- and multiple insecticide resistance (Yasutomi 1966; Hayashi *et al*. 1977; Keiding 1977; Chapman & Morgan 1992; Chapman *et al*. 1993; Learmount, Chapman & MacNicoll 2002). Additionally, in outdoor situations large volumes are needed and spray is likely to drift from the target site. We successfully predicted *M. domestica* numbers from simple and readily recorded weather variables. This could be used to limit prophylactic spraying to periods when climatic conditions are likely to favour fly population increases. Reducing the frequency of spraying may reduce resistance and so render spray applications more effective.

It must be noted that fly catch is likely to be influenced by both fly population size and the weather at the time of sampling, which influences fly activity (Wall, French & Morgan 1992, 1993). If catches are obtained at short time intervals (e.g. every hour) then it is possible to calibrate the catch to take into account the weather, and give a more accurate measure of the underlying fly population (Vogt *et al*. 1983; Vogt 1992). With weekly sampling such as ours the relationship between fly catch and the underlying population cannot easily be resolved, but the accuracy of our models is reassuring in this respect because it suggests that there is a close relationship between the two. However, we have no way of extrapolating from fly catches to obtain a measure of the actual fly density (flies per unit area) in the study areas.

It remains to be tested whether our models accurately predict fly numbers elsewhere, where biotic and abiotic conditions may be different from the sites in our study (for example on livestock farms). If it does not, then predictive models may have to be tailor-made for particular geographical regions or situations. None the less, our data demonstrate that it is possible to obtain reasonably accurate predictions of fly numbers using local meteorological data. We suggest that this approach may be valuable as part of an integrated pest management programme.

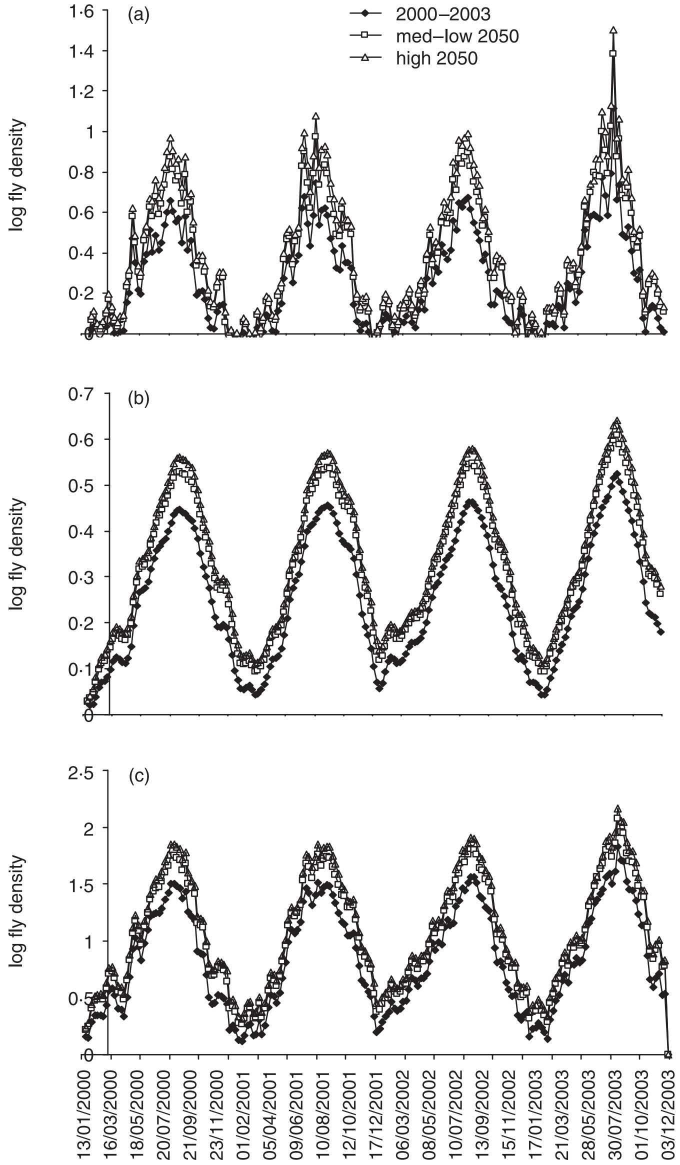

Fig. 3. Actual fly populations for 2000–03 and those predicted by 2050 under two different scenarios of climate change, 'medium–low emissions' and 'high emissions' (from Hulme *et al*. 2002; see Table 7). (a) *Musca domestica*; (b) *Calliphora* spp.; (c) all calyptrate flies.

Our models predict that the temperature rises that are expected to occur within the next few decades may result in substantial increases in numbers of pestiferous flies. Overall, numbers of calyptrate flies are predicted to triple by 2080 under the worst-case scenario, and to double even under the fairly optimistic medium–low emissions scenario. Numbers of *M. domestica*, one of the most troublesome calyptrate species, are predicted to rise even higher. Of course these predictions ignore other climatic changes that may occur but which are less well understood (such as changes in precipitation patterns). As with many other studies that predict increased pest abundance in temperature zones as a result of climate change (Sutherst 1995; Cannon 1998; Baker *et al*. 2000), our predictions do not take into account biotic factors that may alter in the future (for example changes in incidence of fly parasitoids, competitors and pathogens). None the less, it seems likely that fly numbers will increase in the future and that this will lead to increased nuisance value and enhanced transmission of human pathogens unless improved control measures can be devised. Resistance of many fly populations to insecticides is already high and increasing, and many of the more environmentally damaging pesticides are being withdrawn from use. The options available for fly control are becoming fewer at a time when fly populations associated with human habitations and waste are likely to become greater, posing a serious challenge for the future.

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