CSIRO PUBLISHING

Animal Production Science, 2018, **58**, 343–349
http://dx.doi.org/10.1071/AN16112

Predicting nuisance fly outbreaks on cattle feedlots in subtropical Australia

R. M. Godwin[A], *D. G. Mayer*[B], *G. W. Brown*[B], *D. M. Leemon*[B] *and P. J. James*[A,C]

[A]Queensland Alliance for Agriculture and Food Innovation, 306 Carmody Road, The University of Queensland, St Lucia, Qld 4072, Australia.
[B]Agri-Science Queensland, Department of Agriculture and Fisheries, Ecosciences Precinct, 41 Boggo Road, Dutton Park, Qld 4102, Australia.
[C]Corresponding author. Email: p.james1@uq.edu.au

Abstract. Flies are important arthropod pests in intensive animal facilities such as cattle feedlots, with the potential to cause production loss, transmit disease and cause nuisance to surrounding communities. In the present study, seasonal population dynamics of three important nuisance flies, namely house flies (*Musca domestica* L.), bush flies (*M. vetustissima* Walker) and stable flies (*Stomoxys calcitrans* L.) (Diptera: Muscidae), were monitored on cattle feedlots in south-eastern Queensland, Australia, over 7 years. *Musca domestica* was by far the dominant species, comprising 67% of the total flies trapped. Models were developed to assess the relationship between weather parameters and fly abundance and to determine whether population trends could be predicted to improve the timing of control measures. For all three species, there were two main effects, namely time-of-year (mainly reflected by minimum temperatures and solar radiation) and rainfall. The abundance of all three species increased with increasing temperature and rainfall, reaching a peak in summer, before decreasing again. Rainfall events resulted in significantly elevated numbers of *M. domestica* for up to 5 weeks, and for 1 week for *M. vetustissima*. Peak fly numbers were predicted by the model to occur in spring and summer, following 85–90-mm weekly rainfall. The population dynamics of *S. calcitrans* were least influenced by rainfall and it was concluded that weather variables were of limited use for forecasting stable fly numbers in this environment and production system. The models provide a useful tool for optimising the timing of fly-control measures, such as insecticide or biopesticide applications, adding to the efficiency of integrated control programs.

Additional keywords: integrated pest management, *Musca domestica*, *Musca vetustissima*, population dynamics, *Stomoxys calcitrans*.

Received 24 February 2016, accepted 5 August 2016, published online 3 May 2017

Introduction

House flies (*Musca domestica* L.), bush flies (*Musca vestustissima* Walker) and stable flies (*Stomoxys calcitrans* L.) are common nuisance flies associated with intensive animal facilities such as cattle feedlots (Matthiessen 1983; Hogsette *et al*. 2012; Urech *et al*. 2012). Flies can become a significant problem in these areas because of the presence of large amounts of manure and feed in which flies can oviposit and develop. Uncontrolled fly populations constitute a significant nuisance and threaten the health and welfare of livestock, farm workers and surrounding communities through their capacity to transmit pathogens (Graczyk *et al*. 2005; Förster *et al*. 2007, 2009; Ahmad *et al*. 2007; Macovei *et al*. 2007; Baldacchino *et al*. 2013). Control measures may involve various integrated pest-management (IPM) strategies, including feedlot design, management and biological control, but also rely significantly on pesticide applications. However, excessive reliance on pesticide applications is undesirable because of the development of insecticide resistance, potential environmental contamination and health and safety concerns (Wang *et al*. 2012; Khan *et al*. 2013; Scott *et al*. 2013) and IPM strategies are not always optimally utilised.

Abiotic factors such as temperature, moisture and solar radiation have a direct influence on the fecundity and duration of the lifecycle of agriculturally important insects including nuisance flies (Drake 1994), and there are threshold temperatures above and below which different life stages will not develop and survive. Under suitable weather conditions, particularly when favourable temperatures, rainfall and humidity coincide, fly outbreaks can occur in cattle feedlots, even with the best preventative strategies in place. Fly populations can build rapidly to reach problem levels if control measures are left too late, whereas miss-timed precautionary treatments, when fly numbers would not have reached problem levels, needlessly incur labour, treatment costs and increased selection for resistance. Accurately predicting when flies will become a problem would enable the strategic timing of control measures to maximise both effectiveness and cost efficiency of treatments.

Weather parameters have been used to develop models for predicting calyptrate fly numbers in the United Kingdom (*M. domestica* and *Calliphora* spp.; Goulson *et al*. 2005) and for stable flies in Nebraska (Taylor *et al*. 2007). The study by Goulson *et al*. (2005) examined the relationship between fly numbers and weather conditions by using a four year dataset of weekly fly catches and meteorological data in the southern UK. These authors found that fluctuations in fly populations were largely driven by the weather rather than by biotic factors. Predictive models based on rainfall, temperature and humidity were strongly correlated with observed fly numbers (r^2 = 0.52–0.84). For *M. domestica*, temperature in the week before trap collection was the best single predictor, although other aspects of temperature in the preceding 3 weeks also contributed significant predictive power to the model. Weather factors, in particular temperature 0–2 weeks before fly collection and precipitation 3–6 weeks before collection, were also the most important determinants of stable fly populations in Nebraska (Taylor *et al*. 2007). These models were developed in temperate regions of the northern hemisphere and may not be applicable to the subtropical region in Australia where many cattle feedlots are located.

For the present study, several large datasets for fly numbers on feedlots located in subtropical south-eastern Queensland, Australia, collected over 7 years, were used with accompanying weather data from the Queensland Government SILO (Scientific Information for Land Owners) database (https://www.longpaddock.qld.gov.au/silo/, verified 22 June 2015). We investigated the utility and accuracy of predicting periods of high fly numbers, using weather records to facilitate optimal timing of fly-control strategies.

Materials and methods

Adult fly monitoring was conducted in seven feedlots in south-eastern Queensland between October 2001 and April 2008. The feedlots were in three districts, namely Dalby, the Brisbane Valley and Warwick. The historical data were used in conjunction with meteorological data to test the accuracy of predicting fly numbers from different weather variables. The major climatic characteristics of these areas are shown in Table 1 and details of the location of the feedlots, monitoring period and trapping sites are given in Table 2. All seven feedlots were managed according to standard commercial practice. IPM programs for fly control, which included regular fence-line and sedimentation-system cleaning, the release of parasitic wasps (*Spalangia endius*), biopesticides (*Metarhizium anisopliae*) and chemical treatments, were in place on two of the feedlots, while fly-control procedures on the other feedlots included irregular manure removal, insecticide treatments and parasitic wasp releases.

Numbers of the three main nuisance species, namely house flies, bush flies and stable flies, were monitored using alsynite sticky traps (Olson Products, Medina, Ohio, USA) that were supported on stakes 0.9–1.2 m off the ground (Urech *et al*. 2012). The traps were placed within the feedlots at selected sites near manure piles, feed-processing areas, cattle pens, vegetation between pens, the cattle-induction area, silage pits, sedimentation ponds and horse stables. Traps were serviced at intervals of between 1 and 17 days, depending on the time-of-year and fly populations. Trapped flies were brought to the laboratory, identified and counted as per the procedure described in Urech *et al*. (2012).

The Queensland Government SILO database (https://www.longpaddock.qld.gov.au/silo, verified 22 June 2015) was used to provide daily weather data corresponding to the GPS coordinates of each feedlot and the appropriate fly-monitoring period. The SILO database uses historical climate records for Australia and observational records provided by the Bureau of Meteorology (http://www.bom.gov.au/, verified 22 June 2015) together with GPS coordinates, to derive daily datasets for different locations

Table 1. Climate statistics for the Dalby, Brisbane Valley and Warwick districts averaged over the past 20 years

District	Elevation (m)	Annual rainfall (mm)	Average summer temperature (°C)		Average winter temperature (°C)	
			Max	Min	Max	Min
Dalby	344	683	31.7	18.1	19.6	4.9
Brisbane Valley	113	999	30.1	18.9	20.9	7.4
Warwick	477	692	29.5	16.6	18.7	3.7

Table 2. Location and details of fly monitoring at each of the seven southern Queensland feedlots
SCU, standard cattle unit

District and dates of monitoring	Feedlot	Location (GPS)	Carrying capacity (SCU)	Number of trapping sites
Dalby, October 2001 – October 2003	1	27°02′S, 151°20′E	13 000	3–8
Brisbane Valley, November 2004 – April 2008	2	29°24′S, 152°21′E	3100	2–4
	3	27°03′S, 152°18′E	700	1–5
	4	27°06′S, 152°21′E	1000	1–5
Warwick, November 2006 – April 2008	5	28°09′S, 152°06′E	2000	2–4
	6	28°03′S, 151°54′E	1000	1–4
	7	28°06′S, 151°51′E	8000	1–4

that are both spatially and temporally complete. Climate variables used in the construction of models included maximum and minimum temperatures (°C), rainfall (mm), evaporation (mm), solar radiation (MJ/m^2), vapour pressure (hPa), and relative humidity (%) at both the maximum and minimum temperatures.

Data processing and modelling

Daily weather data were converted to weekly data by averaging across each 7-day period. Cumulative weekly totals were calculated for rainfall and evaporation. Fly counts were converted to weekly data by first converting trap data to average flies per trap per day for each monitoring interval and then accumulating the data by date to give weekly counts for each species. These weekly intervals corresponded to the same weekly intervals as for the weather data. The two datasets (weekly fly counts and weekly weather data) were then combined into one dataset for modelling purposes. Data for each fly species were analysed separately using GENSTAT for Windows® v16.1 (GENSTAT 2015).

The $\log_{10}$(catch+1) transformation was adopted for the dependent variables, as these were highly skewed with heterogeneous variance. This implies a multiplicative relationship among the effects of the independent variables, as is biologically expected. The regression models were fitted using residual maximum likelihood (REML) in GENSTAT (2015), with an autoregressive (lag-one) error term to accommodate for the significant autocorrelations between weeks within feedlots. Step-forward, step-backward and all-subsets regressions, plus random forests (multiple regression-tree models; Elith *et al*. 2008) were used to screen the potential predictor variables. Overall shape and degree of curvature of the regression lines were tested using smoothing-spline, non-linear and quadratic models, with the best-fit and biologically appropriate forms adopted for the fitted relationships.

The effects of feedlot treatments were tested using binary contrasts – first as 'overall' (any of the treatments, compared with no treatment), as well as testing the individual types – 'insecticide application' (only tested for the week of application, and the following week), 'parasitic wasps' (only from the second week after the first release) and 'IPM', fitted as an additional effect to the parasitoid-wasp treatment, as wasps were always released as part of IPM, but several feedlots not using IPM also released wasps. The effect of feedlot size on fly numbers was also tested, and was found to be not significant ($P > 0.05$) and was excluded from the model.

There were high degrees of correlation among some weather variables (see Table 3); however, this is not statistically a problem in forecasting when the degrees of correlations are expected to remain approximately similar (Dormann *et al*. 2013). All catch-number results and forecasts were derived using the bias-corrected back-transformation from the log-scale (Kendall *et al*. 1983).

Results

The total number of trapped flies in the present study was 1 185 581, of which 67% were *M. domestica*, 21% were *M. vetustissima* and 12% were *S. calcitrans.* Other fly species, which contributed only a small proportion of the total flies trapped, do not generally breed within the feedlot and, therefore, were not included. Of the three fly species studied, *M. domestica* was most affected by weather variables, showing a higher degree of fit in the derived models than did the other two species.

Table 3. Correlation coefficients (*r*) for the relationships between climate variables included in the initial models

Tmax, maximum temperature; Tmin, minimum temperature; Rain, rainfall; Evap, evaporation; Radn, radiation; VP, vapour pressure; RHx, relative humidity at the maximum temperature; and RHn, relative humidity at the minimum temperature

	Tmax	Tmin	Rain	Evap	Radn	VP	RHx
Tmax	1						
Tmin	0.838	1					
Rain	–0.019	0.260	1				
Evap	0.870	0.669	–0.074	1			
Radn	0.743	0.514	–0.113	0.906	1		
VP	0.782	0.952	0.290	0.542	0.425	1	
RHx	–0.341	0.180	0.506	–0.497	–0.496	0.292	1
RHn	–0.325	–0.163	0.163	–0.538	–0.384	0.075	0.566

Catch data for *M. domestica* for each of the seven feedlots showed that the highest populations occurred in a broad peak during the summer months at all seven feedlots (Fig. 1). Numbers dropped to very low levels during the winter months. All feedlots followed the same trend, although fly numbers in FL 2 in the Brisbane Valley did not decrease to the same extent as those in FL 3 and FL 4 in the winters of 2005 and 2006.

The total numbers of *M. vetustissima* (data not presented) were generally a third of those for *M. domestica*, except in November–December 2007 in the Warwick district (FL 5 and FL 6), where numbers of *M. vetustissima* were 5–10 times higher than those of *M. domestica*. Reasons for the outbreak of *M. vetustissima* are unknown, but probably reflect suitable conditions for bushfly breeding or winds favourable for bushfly immigration to these feedlots (Hughes and Nicholas 1974) at this time. Numbers of *S. calcitrans* trapped were lowest of the three main species, being only about a 10th of those of *M. domestica* and half of those of *M. vetustissima*. Although the population patterns of the three species were generally similar, peak numbers of *M. vetustissima* and *S. calcitrans* occurred slightly earlier in the summer (October to November) than those of *M. domestica*, and then rapidly decreased. Overall, seasonal data showed a strong relationship between the spring–early summer rainfall and increased populations of *M. domestica* (Fig. 2) across years and locations (R^2 = 0.96). Highest fly numbers occurred in the Brisbane valley, which received higher rainfall than did Dalby and Warwick.

Investigations using weekly data showed that, for all species, there were two main climatic effects, namely 'time-of-year' (as best represented by minimum temperatures, or solar radiation) and 'rainfall'. Interactions between the weather terms in the model were minor and not significant ($P < 0.05$). This is probably because the log relationship adopted implicitly accommodates the expected multiplicative relationship between month and rainfall. The 'just weather terms' models had notably high and biased residuals for November and December, indicating that the higher catch rates found in these months

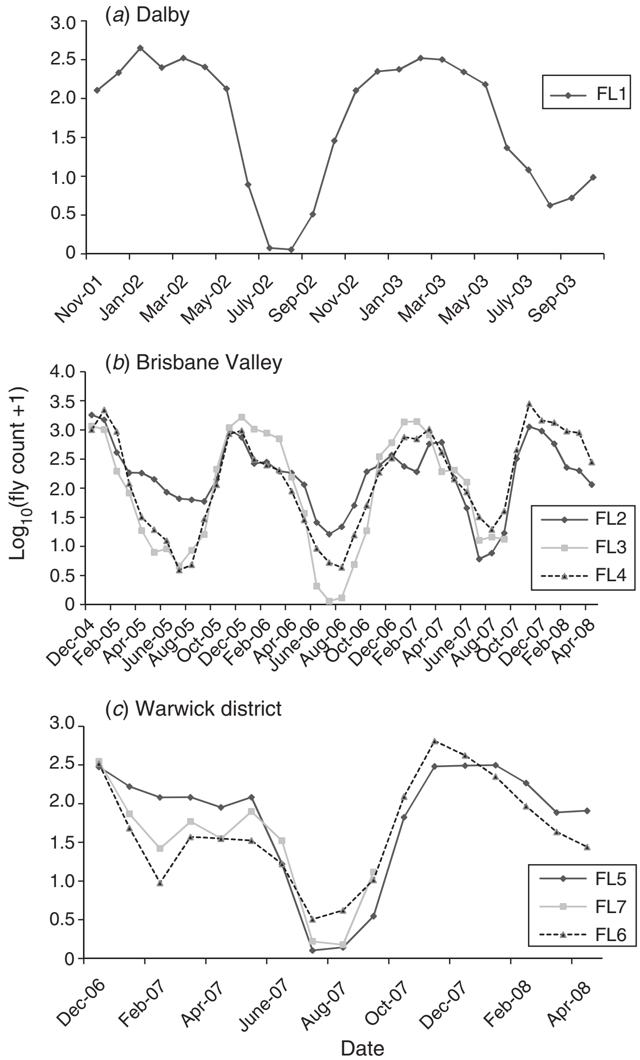

Fig. 1. *Musca domestica* numbers ($\log_{10}$(weekly fly count+1)) for the seven study feedlots (FL) plotted by (*a*) Dalby, (*b*) Brisbane Valley and (*c*) Warwick district.

were not solely explained by the weather terms. Temperatures and rainfall similar to those observed in November and December were also experienced in late summer and autumn (March to May), but fly catch rates then were markedly lower.

Alternative models for the 'time-of-year' effect were investigated, including 'month' (a factor with 12 fixed levels, representing the 'baseline catch rates' for each month) and a Fourier curve. In combination with the rainfall effect, the model with 'month' lifted the degree of fit (adjusted R^2) for *M. domestica* from 61% (for the model with just weather terms) to 69%, and from 31% to 59% for *M. vetustissima*. For *S. calcitrans* the alternative models provided approximately the same level of fit, but month was adopted for consistency.

The shape of the rainfall-effect curve was somewhat difficult to determine, given the generally high degree of variability in catch rates, plus the sparseness of rainfall events with greater than 100 mm per week (there were only nine of these in our dataset). Adopting log rainfall as a linear term, or rainfall as a quadratic effect, produced very similar degrees of fit. For *M. domestica*, the adjusted R^2 values were 68.3% and 68.8% respectively. The quadratic relationship was adopted due to the slightly better fit and better overall agreement with the non-parametric spline models (which indicated a slight depression in catch numbers above ~100 mm per week). Rainfall had extended effects on fly populations, with significant increases in fly numbers persisting for up to 5 weeks after rainfall events. The fitted coefficients were quite consistent, predicting maximum fly numbers at 90, 87, 88, 89 and 99 mm rainfall per week for lags of 1–5 weeks respectively. The fitted relationship for a 3-week lag is shown in Fig. 3.

The effects of feedlot treatments on *M. domestica* populations were mixed. The release of parasitoid wasps had a significant ($P < 0.01$) effect, with the coefficient of –0.2131 (on the $\log_{10}$ scale) translating to a fitted 39% reduction in fly numbers following the release of wasps. IPM had no additional statistical effect on fly numbers over the effect of parasitic-wasp releases, which were always part of the IPM program. There was also no significant effect of insecticide applications on house fly numbers. The non-significant ($P > 0.05$) treatment terms were dropped from the final model, which included only a 'parasitoid-wasp releases' factor.

When months were investigated (as 'time-of-year' effects) in combination with the quadratic rainfall effect for *M. vetustissima*, the degree of fit was significant for a 1-week lag only (adjusted R^2 of 59.1%). The effect of rainfall was greatest between October and December, with little effect for the remainder of the year. Maximum fly numbers were observed after weekly rainfall of 86 mm (Fig. 4), indicating the instant and short-term effect of rain on *M. vetustissima* populations. Feedlot treatments did not significantly affect *M. vetustissima* numbers, although there was an average reduction in catch numbers of 36% ($P = 0.10$) following insecticide sprays.

Stomoxys calcitrans populations were least affected by climate, showing only a low degree of fit ($R^2 = 24.2\%$) when months were investigated in combination with a quadratic rainfall effect for lags of 3, 4 and 5 weeks. There was no significant effect of feedlot treatments, but there was an average reduction of 43% in catch numbers following insecticide applications ($P = 0.09$). The low degree of fit suggests that weather variables were of limited use for forecasting stable fly numbers in this environment and production system.

Discussion

South-eastern Queensland has a subtropical climate with hot, humid summers. Winters are drier, mild to warm, but with cool overnight temperatures. For all fly species, initial screening indicated two main effects on fly numbers, 'time-of-year' (which represents changes in both minimum temperatures and solar radiation) and 'rainfall'. Between April and October, temperature was likely to be the main factor limiting fly numbers. Rainfall had little effect on any of the fly species during the winter months. There are always localised areas in feedlots where moisture is present and flies can breed, and as temperatures rose from October to November, the base number of flies (assuming no rainfall) increased by an average of 352%. The greatest effect of rainfall was seen in the spring and early

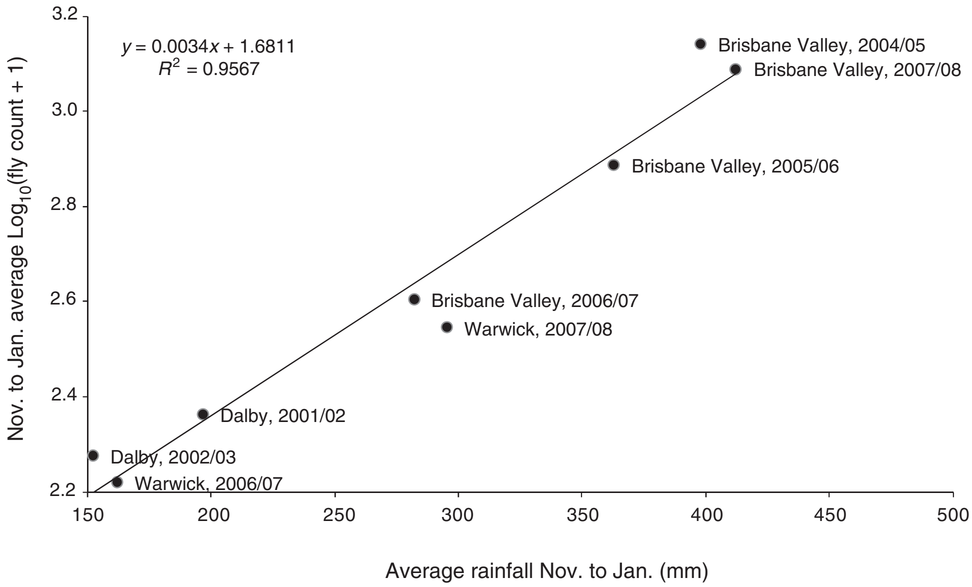

Fig. 2. The relationship between $\log_{10}$ average *Musca domestica* catch rates and rainfall from November to January.

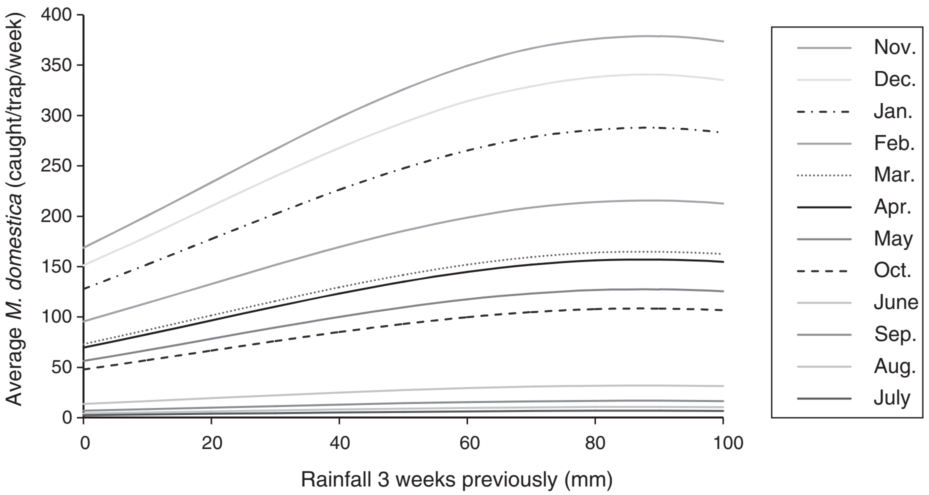

Fig. 3. Fitted values for *Musca domestica* numbers (per trap per week) in response to rainfall 3 weeks previous to trapping for each month of the year.

summer when temperature had increased sufficiently for rapid reproduction and development of flies and the main factor limiting population growth was moisture. The months from November to February were the main period of fly breeding and the model predicted that rainfall of 25 mm would be expected to increase fly numbers by a further 46%, whereas 50 mm could be expected to give an approximate 88% increase in numbers of flies and 90 mm would cause fly numbers to increase by 120%. The model indicated a multiplicative effect of season and rainfall events, suggesting that highest fly numbers would occur following successive rainfall events during early summer.

In contrast to the results reported here, Goulson *et al*. (2005) found that in the UK, temperature was the best predictor of fly numbers. This is not surprising since population dynamics are governed by the 'law of the minimum' and in the temperate wet climate of the UK, temperature rather than moisture is likely to be the limiting factor for a large proportion of the year.

For the major fly species, *M. domestica*, both factors showed extended effect, with significant associations between fly numbers and weather factors measured up to 5 weeks previously. This was not unexpected, as increased moisture has a favourably impact on several different life processes of house flies, including oviposition, egg development and larval survival and development (Williams *et al*. 1985). The period of the effect of rainfall events will also be determined by factors such as the amount of rain received, follow-up rain and environmental influences that affect the rate of drying of the larval habitat, such as soil moisture, humidity and wind. The amount of rainfall predicted to produce maximum *M. domestica* numbers with lags of 1, 2, 3, 4 and 5 weeks was remarkably

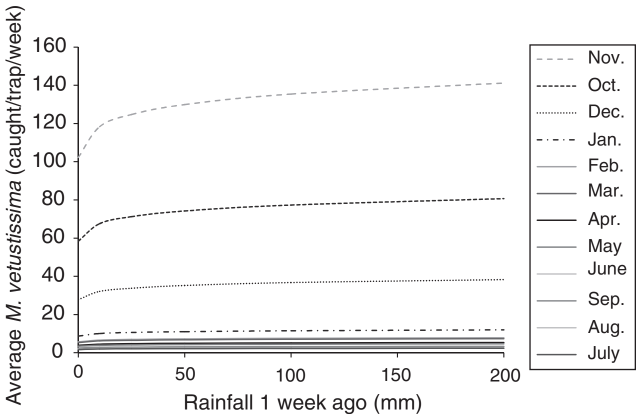

Fig. 4. Fitted values for *Musca vetustissima* numbers (per trap per week) in response to rainfall 1 week previous to trapping for each month of the year.

consistent at 90, 87, 88, 89 and 99 mm/week respectively. The scarcity of higher rainfall events during the period of the study did not allow us to accurately extrapolate the effects of rainfall above 100 mm, but the shape of the rainfall–fly numbers curves suggests that there is a maximal level of rain for fly production, above which further increases in fly numbers do not occur. Weekly rainfall above this level may be detrimental to fly populations by causing drowning or suffocation of fly larvae, pupae and eggs (Farkas *et al*. 1998).

Higher *M. domestica* catches were recorded in the months of November and December than during months with similar rainfall and temperatures later in summer. This is likely to be due to the effects of predators and parasites. When conditions become favourable, flies build up very rapidly. However, predators and parasites that feed on or parasitise flies generally breed more slowly and take some time 'to catch up' and exert a regulating influence on fly numbers. Later in the season, it is likely that there are more predators and parasites present and these have a greater effect in suppressing fly populations than earlier in the year. This hypothesis is supported by the significant effect of augmentative releases of parasitoids in suppressing fly numbers seen in the present study, and similar effects noted with flies breeding in poultry facilities (Peck and Anderson 1970; James *et al*. 2016).

The effect of rainfall was less pronounced on *M. vestustissima*, with falls of 85 mm having a relatively instant, but short-term, effect on fly numbers. The short-term effect is not surprising, since *M. vetustissima* breeds mainly in manure pats outside the feedlot area. These dry out more quickly than do the large accumulations of manure present within feedlots. Increases in *M. vestustissima* abundance in the feedlots may have been the result of immigrant flies being attracted to the feedlots by moisture, odours and potential protein sources (Hughes *et al.* 1972). The effect of spraying was more pronounced with *M. vetustissima* than house flies and this was probably because few bush flies emerge from pupae within feedlots, whereas house fly populations are supplemented daily by flies emerging on site. In addition, resistance is known to be widespread in *M. domestica* populations worldwide. This was not assessed in the present project, but may also have contributed to the lack of effect from spraying noted in the study.

Numbers of *S. calcitrans* were less affected by weather variables than were those of either *M. domestica* or *M. vestustissima*. A previous study in a similar location showed that although both house flies and stable flies originated mainly from within the feedlot area, *M. domestica* was found mainly in areas containing animals and feed, whereas the highest catches of *S. calcitrans* were near the feed mill, silage pits and piled manure (Urech *et al*. 2012). *S. calcitrans* breeds mostly in spilled feed or mixtures of dung and decaying fibrous material (Meyer and Petersen 1983; Hogsette *et al.* 1987; Dawit *et al*. 2012) and numbers of this species are largely determined by the availability of these resources.

Seasonal patterns of *S. calcitrans* abundance observed in other studies have been highly variable depending on location, climatic conditions and management regime (Lysyk 1993; Taylor *et al*. 2007; Skovgård and Nachman 2012; Jacquiet *et al*. 2014). Temperatures above 30°C have been found to have a negative impact on *S. calcitrans*, (Lysyk 1998; Gilles *et al*. 2005; Skovgård and Nachman 2012), which may explain the reduction in fly numbers observed in the present study during the hot summer months. Additionally, Urech *et al.* (2012) found that *S. calcitrans* was more abundant on central New South Wales feedlots, which were located 4–8° further south and had lower summer temperatures than did feedlots in southern Queensland.

Taylor *et al*. (2007) developed population models for *S. calcitrans* based on temperature and precipitation and found that temperatures 0–2 weeks before collection and precipitation 3–6 weeks before collection were the most important variables influencing stable fly numbers. During midsummer, precipitation, not temperature, was the major factor limiting stable fly populations. However, the major source of stable flies in their study was from pastures and, more particularly, sites where large round hay bales were fed to cattle. Thus, their model was developed in a cattle-management system that was quite different from that in the present study. They noted that the relationship between weather variables and fly numbers would likely vary depending on larval development sites, climatic zone and cultural conditions, and highlighted the need for predictive models to be substantiated under a range of conditions to determine their universality.

The models developed here will provide useful tools to assist with timing of the application of insecticides or biopesticides for fly control in feedlots of south-eastern Queensland. The models suggest that fly treatments will seldom be justified during months from March to October. As the models are based on 7 years of data obtained from seven feedlots distributed across an area of ~15 000 km^2, they are likely to have application at least at a regional level and in other areas of the world with a similar subtropical climate. Whether or not to treat and after what amount of rainfall treatments should be applied will depend on individual tolerances to fly numbers, management circumstances and the perceived likelihood of follow-up rainfall and temperatures to sustain fly breeding. However, the 'rules of thumb' presented here, used within an integrated control program and adapted to individual feedlot circumstances, will enable much more targeted application of pesticide treatments, reducing the cost and the undesirable effects of unneeded treatments and providing more efficient fly control.

Acknowledgements

We thank Dr Rudolf Urech, Mr Peter Green and their project team for their significant contribution in conducting the two projects that generated the data and provided the basis of this paper. These projects were funded by Meat and Livestock Australia (MLA) and their support is gratefully acknowledged by the authors. We also acknowledge the owners, managers and staff of the feedlots in the Dalby, Warwick and Brisbane Valley areas for their cooperation and interest in these projects.

References

Ahmad A, Nagaraja TG, Zurek L (2007) Transmission of *Escherichia coli* O157:H7 to cattle by houseflies. *Preventive Veterinary Medicine* **80**, 74–81. doi:10.1016/j.prevetmed.2007.01.006

Baldacchino F, Muenworn V, Desquesnes M, Desoli F, Charoenviriyaphap T, Duvallet G (2013) Transmission of pathogens by *Stomoxys* flies (Diptera, Muscidae): a review. *Parasite* **20**, 26. doi:10.1051/parasite/2013026

Dawit L, Addis M, Gari G (2012) Distribution, seasonality and relative abundance of *Stomoxys* flies in selected districts of central Ethiopia. *World Applied Sciences Journal* **19**, 998–1002.

Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carré G, Marquéz JRG, Gruber B, Lafourcade B, Leitão PJ (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46. doi:10.1111/j.1600-0587.2012.07348.x

Drake V (1994) The influence of weather and climate on agriculturally important insects: an Australian perspective. *Crop and Pasture Science* **45**, 487–509. doi:10.1071/AR9940487

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *Journal of Animal Ecology* **77**, 802–813. doi:10.1111/j.1365-2656.2008.01390.x

Farkas R, Hogsette J, Borzsonyi L (1998) Development of *Hydrotaea aenescens* and *Musca domestica* (Diptera: Muscidae) in poultry and pig manures of different moisture content. *Environmental Entomology* **27**, 695–699. doi:10.1093/ee/27.3.695

Förster M, Klimpel S, Mehlhorn H, Sievert K, Messler S, Pfeffer K (2007) Pilot study on synanthropic flies (eg *Musca, Sarcophaga, Calliphora, Fannia, Lucilia, Stomoxys*) as vectors of pathogenic microorganisms. *Parasitology Research* **101**, 243–246. doi:10.1007/s00436-007-0522-y

Förster M, Sievert K, Messler S, Klimpel S, Pfeffer K (2009) Comprehensive study on the occurrence and distribution of pathogenic microorganisms carried by synanthropic flies caught at different rural locations in Germany. *Journal of Medical Entomology* **46**, 1164–1166. doi:10.1603/033.046.0526

GENSTAT (2015) 'GENSTAT for Windows.' (VSN International: Oxford, UK)

Gilles J, David J-F, Duvallet G (2005) Temperature effects on development and survival of two stable flies, *Stomoxys calcitrans* and *Stomoxys niger* niger (Diptera: Muscidae), in La Reunion island. *Journal of Medical Entomology* **42**, 260–265. doi:10.1603/0022-2585(2005)042[0260:TEODAS]2.0.CO;2

Goulson D, Derwent LC, Hanley ME, Dunn DW, Abolins SR (2005) Predicting calyptrate fly populations from the weather, and probable consequences of climate change. *Journal of Applied Ecology* **42**, 795–804. doi:10.1111/j.1365-2664.2005.01078.x

Graczyk TK, Knight R, Tamang L (2005) Mechanical transmission of human protozoan parasites by insects. *Clinical Microbiology Reviews* **18**, 128–132. doi:10.1128/CMR.18.1.128-132.2005

Hogsette JA, Ruff JP, Jones CJ (1987) Stable fly biology and control in northwest Florida. *Journal of Agricultural Entomology* **4**, 1–11.

Hogsette J, Urech R, Green P, Skerman A, Elson-Harris M, Bright R, Brown G (2012) Nuisance flies on Australian cattle feedlots: immature populations. *Medical and Veterinary Entomology* **26**, 46–55. doi:10.1111/j.1365-2915.2011.00981.x

Hughes RD, Nicholas WL (1974) The spring migration of the bushfly (*Musca vetustissima* Walk.): evidence of displacement provided by natural population markers including parasitism. *Journal of Animal Ecology* **43**, 411–428. doi:10.2307/3373

Hughes RD, Greenham PM, Tyndale Biscoe M, Walker JM (1972) A synopsis of observations on the biology of the Australian bushfly (*Musca vetustissima* Walker). *Journal of the Australian Entomological Society* **11**, 311–331. doi:10.1111/j.1440-6055.1972.tb01635.x

Jacquiet P, Rouet D, Bouhsira E, Salem A, Lienard E, Franc M (2014) Population dynamics of *Stomoxys calcitrans* (L.) (Diptera: Muscidae) in southwestern France. *Revue de Medecine Veterinaire* **165**, 267–271.

James PJ, Krawek C, Schellhorn NA, Glatz PC, Pepper PM (2016) Species composition and dispersal of nuisance flies breeding on egg farms in southern Australia. *Animal Production Science.* doi:10.1071/AN14939

Kendall M, Stuart A, Ord JK (1983) 'The advanced theory of statistics.' (Griffin: London)

Khan HAA, Shad SA, Akram W (2013) Resistance to new chemical insecticides in the house fly, *Musca domestica* L., from dairies in Punjab, Pakistan. *Parasitology Research* **112**, 2049–2054. doi:10.1007/s00436-013-3365-8

Lysyk T (1993) Seasonal abundance of stable flies and house flies (Diptera: Muscidae) in dairies in Alberta, Canada. *Journal of Medical Entomology* **30**, 888–895. doi:10.1093/jmedent/30.5.888

Lysyk T (1998) Relationships between temperature and life-history parameters of *Stomoxys calcitrans* (Diptera: Muscidae). *Journal of Medical Entomology* **35**, 107–119. doi:10.1093/jmedent/35.2.107

Macovei L, Miles B, Zurech L (2007) Potential of houseflies to contaminate ready-to-eat food with antibiotic-resistant enterococci. *Journal of Food Protection* **71**, 435–439.

Matthiessen JN (1983) The seasonal distribution and characteristics of bush fly *Musca vetustissima* Walker populations in south-western Australia. *Australian Journal of Ecology* **8**, 383–394. doi:10.1111/j.1442-9993.1983.tb01335.x

Meyer J, Petersen J (1983) Characterization and seasonal distribution of breeding sites of stable flies and house flies (Diptera: Muscidae) on eastern Nebraska feedlots and dairies. *Journal of Economic Entomology* **76**, 103–108. doi:10.1093/jee/76.1.103

Peck JH, Anderson JR (1970) Influence of poultry manure-removal schedules on various Diptera larvae and selected arthropod predators. *Journal of Economic Entomology* **63**, 82–90. doi:10.1093/jee/63.1.82

Scott JG, Leichter CA, Rinkevihc FD, Harris SA, Su C, Aberegg LC, Moon R, Geden CJ, Gerry AC, Taylor DB (2013) Insecticide resistance in house flies from the United States: resistance levels and frequency of pyrethroid resistance alleles. *Pesticide Biochemistry and Physiology* **107**, 377–384. doi:10.1016/j.pestbp.2013.10.006

Skovgård H, Nachman G (2012) Population dynamics of stable flies *Stomoxys calcitrans* (Diptera: Muscidae) at an organic dairy farm in Denmark based on mark–recapture with destructive sub-sampling. *Environmental Entomology* **41**, 20–29. doi:10.1603/EN11155

Taylor DB, Berkebile DR, Scholl PJ (2007) Stable fly population dynamics in eastern Nebraska in relation to climatic variables. *Journal of Medical Entomology* **44**, 765–771. doi:10.1093/jmedent/44.5.765

Urech R, Bright RL, Green PE, Brown GW, Hogsette JA, Skerman AG, Elson-Harris MM, Mayer DG (2012) Temporal and spatial trends in adult nuisance fly populations at Australian cattle feedlots. *Australian Journal of Entomology* **51**, 88–96. doi:10.1111/j.1440-6055.2011.00846.x

Wang Q, Li M, Pan J, Di M, Liu Q, Meng F, Scott JG, Qiu X (2012) Diversity and frequencies of genetic mutations involved in insecticide resistance in field populations of the house fly (*Musca domestica* L.) from China. *Pesticide Biochemistry and Physiology* **102**, 153–159. doi:10.1016/j.pestbp.2011.12.007

Williams RE, Hall RD, Broce AB, Scholl PJ (1985) 'Livestock entomology.' (John Wiley & Sons)