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Predicting the geographic distribution of *Lucilia sericata* and *Lucilia cuprina* (Diptera: Calliphoridae) in South Africa

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ABSTRACT

Lucilia sericata (Meigen, 1826) and *Lucilia cuprina* (Wiedemann, 1830) (Diptera: Calliphoridae: Luciliinae) have medical, veterinary and forensic importance. Knowing their distribution in South Africa would allow more effective management and utilisation of these flies. Their predicted geographic distributions in South Africa were modelled using maximum entropy analysis of selected climatic variables. The most important environmental variables in modelling the distributions were the magnitude of monthly rainfall and the magnitude of the monthly maximum temperature for *L. sericata* and the seasonal variation in monthly mean humidity and magnitude of monthly rainfall for *L. cuprina*. A clear geographical bias was shown in museum records and supports the need for focused surveys. There was no correlation between the predicted distribution of *L. cuprina* and sheep farming in South Africa, nor between the predicted distribution of *L. sericata* and human population density. Although their patterns of occurrence differed, both species are widely distributed in South Africa and therefore one cannot identify these flies by locality alone – morphological or molecular identification is necessary.

KEY WORDS: Calliphoridae, *Lucilia cuprina*, *Lucilia sericata*, blowflies, environmental variables, MaxEnt, modelling.

INTRODUCTION

Lucilia sericata (Meigen, 1826) is a cosmopolitan greenbottle blowfly that originates from Europe and which is used in maggot debridement therapy (MDT) – the use of maggots to clean necrotic wounds on living human beings (Sherman *et al*. 2000; Wolff & Hansson 2005; Williams *et al*. 2008; Altincicek & Vilcinskas 2009; Paul *et al*. 2009; Tantawi *et al*. 2010). The maggots are also important in forensic entomology (Louw & van der Linde 1993; Smith & Wall 1997; Anderson 2000; Oliva 2001; Clark *et al*. 2006; Day & Wallman 2006) and, to a lesser extent, in sheep strike – the process whereby these flies lay their eggs on living sheep and the maggots damage the wool and skin by feeding on the sheep (Hepburn 1943; Ullyett 1945; Vogt & Woodburn 1979; Heath & Bishop 2006). It has been suggested that in South Africa, *L. sericata* occurs in urban areas and is not found in rural settings (Meskin 1986; Braack & de Vos 1987). *Lucilia cuprina* (Wiedemann, 1830), its sister species, is indigenous to Africa and Asia. It is a huge problem in sheep strike (Hepburn 1943; Ullyett, 1945; Vogt & Woodburn 1979; Heath & Bishop 2006), has been successfully used in MDT (Paul *et al*. 2009; Tantawi *et al*. 2010), and is useful in forensic investigations (Louw & van der Linde 1993; Day & Wallman 2006). It is thought that in South Africa, this species occurs primarily in rural environments and seldom near human habitation (Meskin 1986; Braack & de Vos 1987). Both species have the potential to spread disease because they breed in decaying and rotting organic matter (Zumpt & Patterson 1952).

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To understand these flies for forensic investigations and veterinary research, one needs to know where they occur, both locally and country-wide. Knowing their geographic distribution would also assist in developing strategies to control fly strike in sheep-farming areas. Mapping the distribution of *L. sericata* is complicated by it being an introduced species to the country, and that it may still be in the process of spreading to the limits of its potential distribution. In this situation, old maps need to be updated with new distribution records. Climate change creates a greater challenge for understanding both species because changing conditions at a locality may alter its suitability for either species, so that old historical locality records eventually need to be revised.

Species distribution modelling techniques produce maps of the potential distribution of species (Elith & Leathwick 2009). MaxEnt (Phillips *et al*. 2006; Phillips & Dudík 2008) is a predictive biogeography programme that uses a maximum entropy algorithm to match known locality points for a species to potential localities, based on their environmental characteristics. It is a useful technique because it does not require absence records to build a predictive model. This allows one to use museum and other occurrence records without having to do fieldwork to provide absence records, which is costly, time-consuming and often ambiguous in outcome (Phillips & Dudík 2008).

In this paper, we present models of predicted geographic distributions for *L. sericata* and *L. cuprina* in South Africa and discuss the environmental variables highlighted by these models. The correlations between where these species are predicted to occur and the distribution of sheep farming and human settlements are also examined.

MATERIAL AND METHODS

Locality records

Historical occurrence records for *Lucilia sericata* and *Lucilia cuprina* were obtained from the following museums: KwaZulu-Natal Museum (formerly the Natal Museum, Pietermaritzburg); Albany Museum (Grahamstown); Iziko Museum (formerly the South African Museum, Cape Town); Durban Natural Science Museum (Durban) and the National Museum (Bloemfontein). The identifications of the specimens were confirmed by the authors. Indeterminable specimens were excluded. Ten additional records with co-ordinates were obtained from literature surveys (Braack 1986; Braack & de Vos 1987; Louw & van der Linde 1993).

Current occurrence records were obtained from personal contacts (see acknowledgements) and from five collecting surveys, undertaken following the literature survey and after museum records had been obtained, to collect data from poorly-sampled and under-represented areas of the country. Traps were set at ~50 km intervals along the chosen route (Fig. 1A & B) and left for four days. They were placed in rural areas along the roadside, at least 2 km away from towns and out of sight of human settlements. Field trips were conducted year-round except during winter (May to August), when blowfly numbers are known to be low (Williams 2002). Redtop™ fly traps (Miller Methods, Ltd) were modified by removing the base of the traps and attaching screw-top jars containing fresh chicken liver to them (Fig. 2). The centres of the jars' lids were cut out and the mouth of the jars covered by netting. The jars were then screwed on to the plastic base of the traps with the lids. This allowed flies to detect the odour of the bait and enter the trap, but prevented them from getting to the bait and thus becoming too fouled to identify. The flies were therefore confined to the bag of the trap and were easily removed.

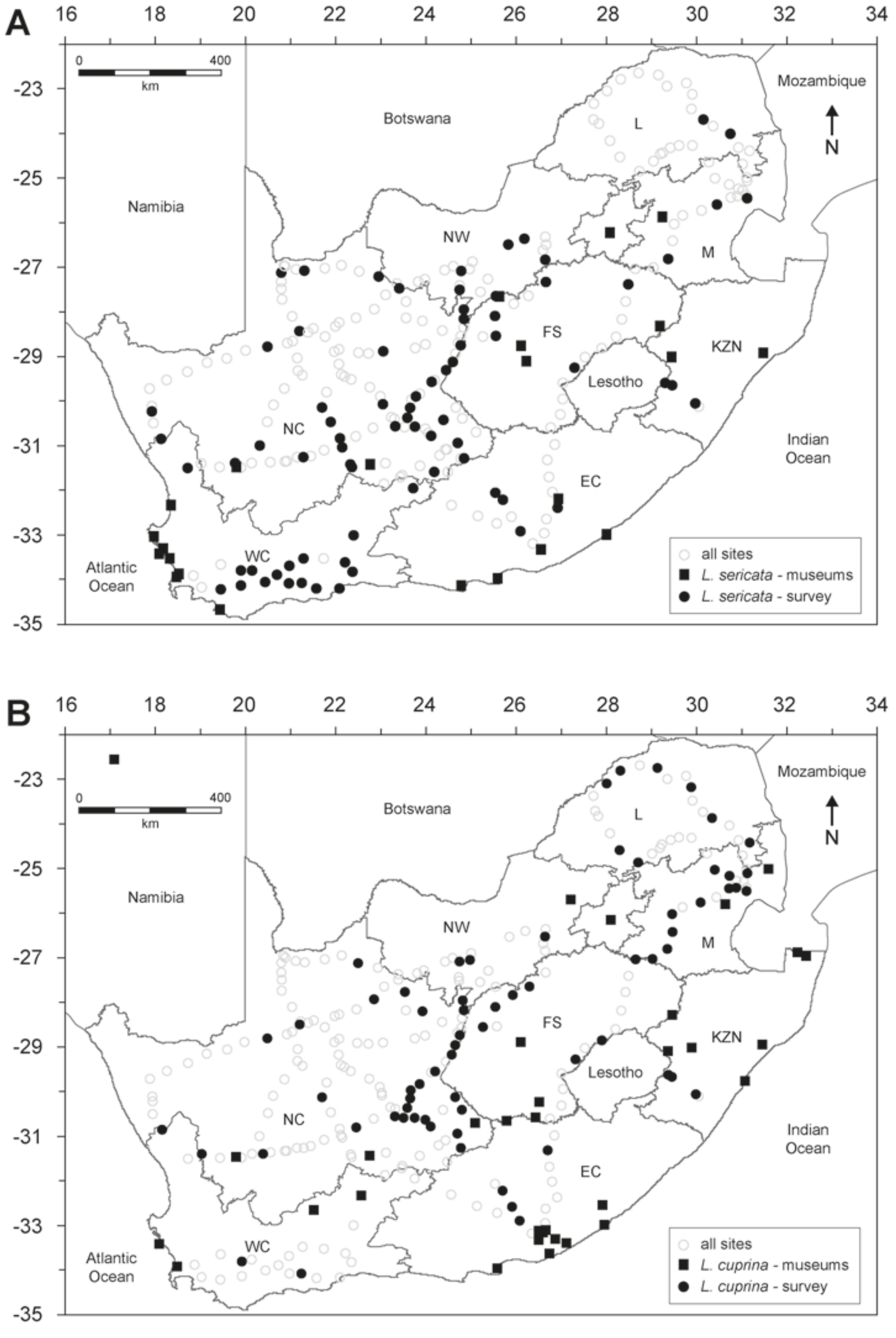

Fig. 1. Map of South Africa, showing the occurrence records and collection trip routes for (A) *Lucilia sericata* and (B) *Lucilia cuprina*.

Fig. 2. Modified Red-top™ fly trap used in surveys.

A total of 132 records (60 collection and 72 survey records) were obtained for *L. cuprina* and 120 (39 collection and 81 survey records) for *L. sericata.* There were several survey sites where both or either species were not recorded (Fig. 1A & B). No museum or literature records more than 50 years old were used for the analysis, as these are not within the temporal span of the climatic variables used in this study (Schulze *et al*. 1997). Duplicated site records were not taken into account so as to prevent pseudoreplication.

Environmental variables

Eleven climatic predictor variables were selected for building the models. These represented variables that are regarded as appropriate to ectotherms at global and regional scales (Mackey & Lindenmayer 2001; Phillips 2008; Richards *et al*. 2009). No vegetation variables were included because these flies are habitat generalists and do not require a particular type of vegetation to breed, although they probably do not occur in forests. It was anticipated that climatic variables would have the greatest abiotic influence on their distribution (Meskin 1986; Braack & de Vos 1987; Williams 2002). Digital maps

TABLE 1
Mean area-under-curve (AUC) values for whole models.

	AUC	
	Lucilia sericata	*Lucilia cuprina*
Training data	0.78	0.77
Test data	0.69	0.69
Standard deviation	0.0489	0.0471

of the variables for South Africa were developed by Schulze *et al*. (1997) to produce continuous digital maps at a resolution of 60 pixels per degree (i.e. about 1.6 x 1.6 km) by interpolating from point data obtained from a network of weather stations throughout South Africa and averaged over 10 years (Schulze *et al*. 1997). Principal component analyses (PCA) were performed on the climatic variable maps as per Richards *et al*. (2009), which resulted in two summary layers for each variable (Table 1). The first variable generally represents the magnitude of the climatic variable while the second generally represents the seasonal variation of the variable (Richards *et al*. 2009).

Model building

MaxEnt 3.3.3k software was used as it requires only presence records and its efficacy has been well documented (Elith *et al*. 2006; Phillips *et al*. 2006; Phillips & Dudík 2008). The default parameters of MaxEnt were used (Phillips & Dudík 2008). These included the regularization multiplier (1), maximum number of iterations (500), maximum number of background points (10 000) and convergence threshold (0.00001). Only hinge features were used as this avoids the overfitting of MaxEnt models when dealing with alien species (Elith *et al*. 2010); and 25 % of the data were reserved to test the model. The outputs of ten replicates were combined to give a mean output. A logistic output for constructing the predictive maps was selected as it is the easiest to comprehend, giving a value between 0 and 1 as the probability of occurrence of an organism (Phillips & Dudík 2008). Jackknife analyses and mean area-under-curve (AUC) plots were created using MaxEnt. AUC is commonly used as a test of the overall performance of the model (Elith *et al*. 2006) and although reservations have been expressed about its utility (Lobo *et al*. 2008), it remains a handy indication of the usefulness of a model (Elith *et al*. 2006, 2011). A value of 1.00 is perfect agreement with the model, while a value of 0.50 represents a random fit. Jackknife analysis indicates which variable has the greatest influence on the model and the overall success of the model.

The data were then divided into survey records and museum records and each partition was modelled separately to assess the importance of doing a focused survey.

Post hoc comparisons

To examine the putative relationship of each species to sheep strike, data for wool production in South Africa for 2011/2012 were obtained from Cape Wools SA and mapped to the magisterial district level as kg/km² (Fig. 3) to show the areas of highest density of sheep farming in South Africa. The average predicted likelihood values from the MaxEnt models for both *L. sericata* and *L. cuprina* at a magisterial district level were plotted against the values for wool production and the correlation coefficient was calculated using PAST3 (Hammer *et al*. 2001) (Fig. 5A & B).

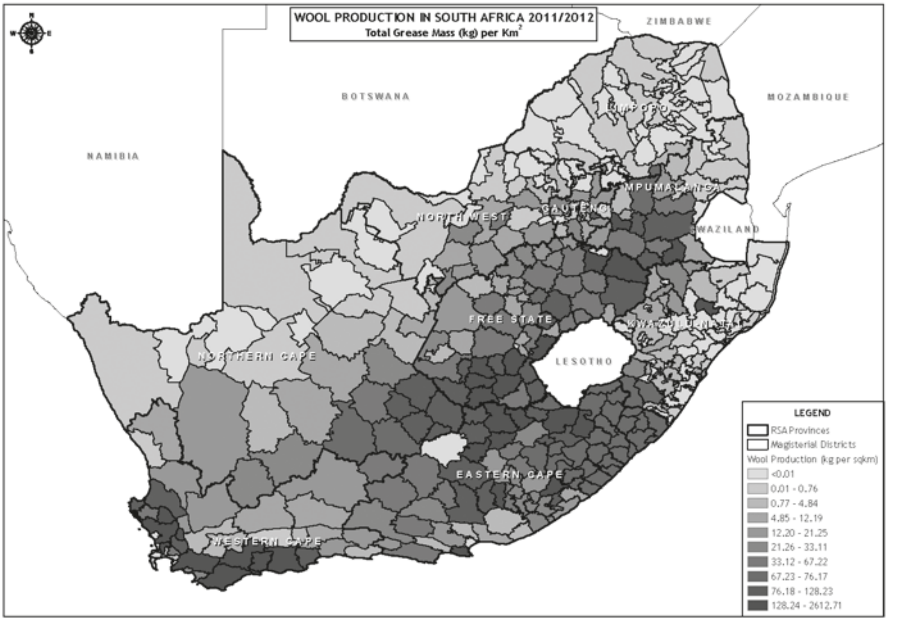

Fig. 3. Wool production of magisterial districts, estimated by total grease mass produced in 2011/2012 in South Africa.

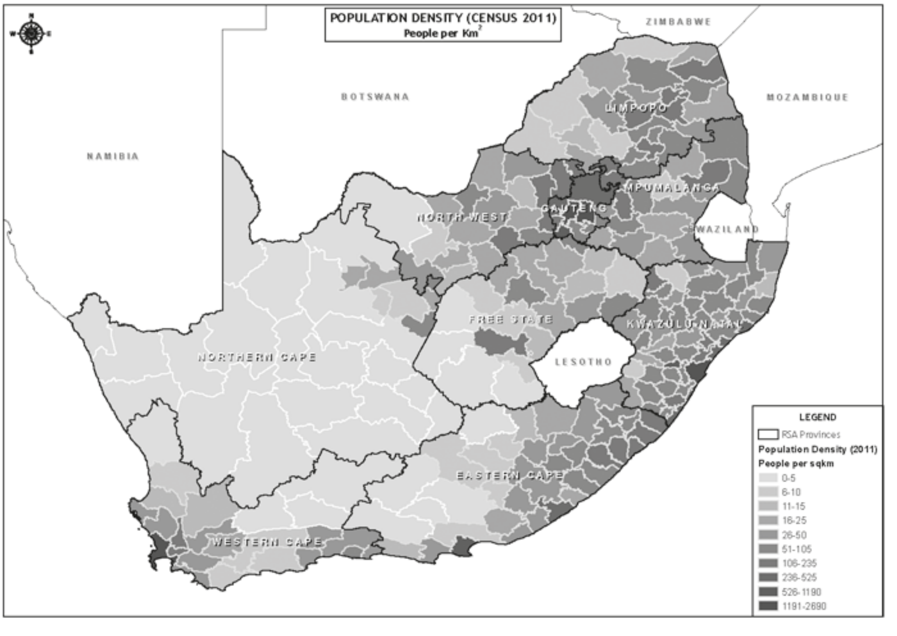

Fig. 4. Distribution of human population in South Africa in 2011 in terms of density.

To evaluate the putative synanthropy of *L. sericata*, human population density figures for South Africa were obtained from the 2011 national census results. These data were mapped as people/km² at the municipal level (Fig. 4). The average predicted likelihood values from the MaxEnt models for both *L. sericata* and *L. cuprina* were plotted against the values for the population density figures at a municipal level and the correlation coefficient was calculated using PAST3 (Hammer *et al*. 2001) (Fig. 5C & D). This allowed quantitative comparison between the areas of highest human habitation and the predicted distribution of the flies.

RESULTS

It is predicted that both species occur in large areas of South Africa (Fig. 6A & B). *Lucilia sericata* has a predicted central and western distribution, with a very low likelihood of occurring in the northern parts of South Africa. *Lucilia cuprina* has mainly a central and eastern predicted distribution, but it also includes the northern parts of South Africa. The mean area-under-curve (AUC) for *L. sericata* and *L. cuprina* was 0.78 and 0.77, respectively, for the training model and 0.69 for both test models (Table 1), indicating moderately good fits of the models to the data.

Jackknife analysis showed that the magnitude of monthly rainfall and the magnitude of the maximum monthly temperature were the most important climatic variables predicting the distribution of *L. sericata* (Fig. 7A). The seasonal variation in humidity and magnitude of monthly rainfall were the most important predictors for *L. cuprina* (Fig. 7B).

The museum data models (Fig. 8A & C) show distinctly different areas of suitability for both *L. sericata* and *L. cuprina* when compared to the survey data models for the same species (Fig. 8B & D).

The comparison between the predicted distribution of *L. sericata* and wool production in South Africa showed no correlation ($r = 0.067$; $p = 0.190$) between where this species is predicted to occur and where there are large numbers of sheep because of wool farming (Figs 3, 5B & 6A). The comparison between *L. cuprina* and wool production also revealed no correlation ($r = 0.017$; $p = 0.735$) between sheep-farming areas and the predicted areas in which this species is likely to occur (Figs 3, 5A & 6B).

The comparison between the predicted distribution of *L. sericata* and human population density distribution showed no correlation ($r = 0.102$; $p = 0.121$). Large areas of low population density in the Northern Cape were predicted to be areas suitable for this species, whereas areas of high population density in Limpopo and eastern Mpumalanga were areas of low suitability for this species (Figs 4, 5D & 6A).

The predicted distribution of *L. cuprina* showed no statistically significant correlation ($r = 0.019$; $p = 0.769$) with human settlement despite areas of high population density, particularly in the Western Cape and eastern parts of South Africa (Figs 4, 5C & 6B), being areas of higher suitability for this species.

DISCUSSION

The maximum entropy modelling technique has been used to model plant and insect distributions for purposes such as monitoring invasive species and disease vectors and their potential spread due to climate change (Chamaillé *et al*. 2010; Kulkarni *et al*.

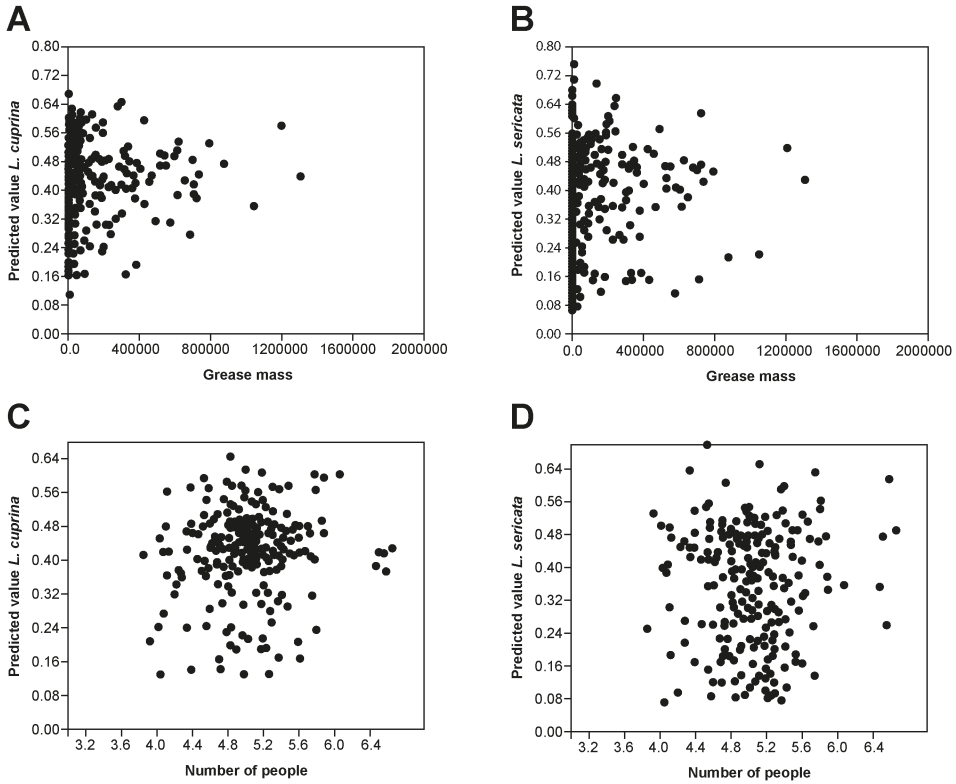

Fig. 5. Plots showing the correlation between the predicted distribution of *Lucilia cuprina* (A & C) and *Lucilia sericata* (B & D) to grease mass (kg) and human population density values (log values).

2010; Fischer *et al*. 2011; Gormley *et al*. 2011; Gurgel-Gonçalves *et al*. 2012; Petersen 2013). It performs well on small sample sizes (Pearson *et al*. 2007), which indicates that the generative methods used in MaxEnt give better predictions than the discriminative methods employed by other techniques (Elith *et al*. 2006; Phillip & Dudík 2008).

The mean AUC for the species models is on the low side (0.69 for both species); models with values above 0.75 are considered potentially useful (Elith 2002). This could be explained by the fact that the validity of models is more uncertain when species show temporal or spatial variation in their habitats; or are tolerant of a wide variety of habitats or have large distributional ranges; or are are migrants or nomadic (McPherson & Jetz 2007). Blowflies are typically r-selected (Elzinga 1997), mobile opportunists (Smith & Wall 1998) that make use of most available carrion resources to breed (Richards *et al*. 2009). This means that they may occur in an area as a result of factors other than the local environmental variables used in this study, e.g. transient food and breeding resources.

By using climatic variables for predicting species distributions, the assumption is made that those variables actually define the limits of the distribution of the species. Other factors, like geographic barriers and biotic interactions, may limit the species so that it does not or cannot occupy all of the climatically suitable areas (Meskin 1986; Soberón

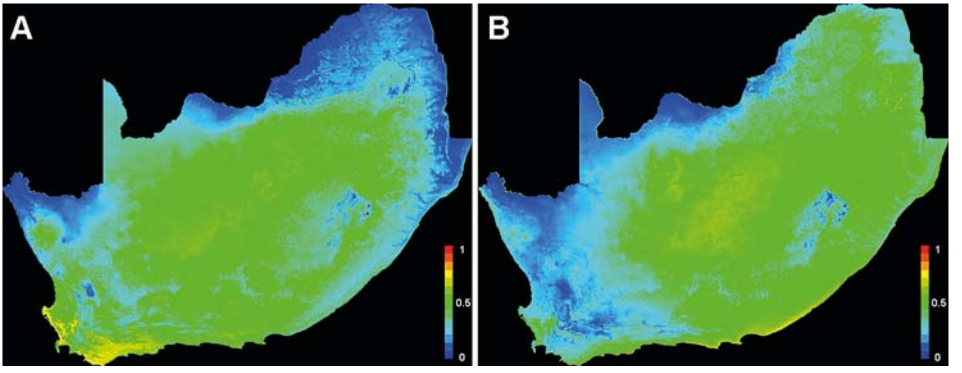

Fig. 6. Mean predicted distribution maps for *Lucilia sericata* (A) and *Lucilia cuprina* (B), produced using museum records, survey data and personal contact localities. The colour range indicates the likelihood of species distribution from dark blue (least likely) to red (most likely).

& Peterson 2005; Pearson *et al*. 2007). Certain ecological traits such as physiological tolerance and home range size exert real effects on the accuracy of distribution models that are not explained by methodology (McPherson & Jetz 2007). MaxEnt predicts potential distributions, not realised ones (Phillips & Dudík 2008), which means that some areas may be predicted to be suitable for these blowflies based on the environmental variables used, yet the flies are not found in those areas because there are other factors, such as competition with other blowflies, for resources that may affect their ability to survive in those areas.

The model for *L. sericata* is most influenced by the magnitude of monthly rainfall and the magnitude of the maximum monthly temperatures (Fig. 7A). This species originated in Europe and has been present in South Africa for over 100 years (museum records). Braack & Retief (1986) showed that the blowflies *Chrysomya albiceps* (Wiedemann, 1819) and *C. marginalis* (Wiedemann, 1830) were able to travel up to 2.25 km/day. Some of these flies dusted with radioactive P-powder were recovered as far as 63.5 km from the release site. In Australia, fluorescent dusted *L. cuprina* were found 17 km from the release point (Gilmour *et al.* 1946). This supports the idea that *L. sericata* has spread throughout South Africa to all the niches it can inhabit. The east coast and northern parts of South Africa are generally hotter (Schulze *et al*. 1997), which appears to limit the likelihood of this species occurring in these regions. Although *L. sericata* is an introduced species, we do not believe that there are any major barriers to its dispersal in South Africa. The rate at which *Chrysomya megacephala* (Fabricius, 1794) was recorded as spreading in South Africa after being introduced in 1971, suggests that blowflies are capable of doing so very rapidly in the country, likely because of their r-selected reproductive biology (Williams & Villet, 2006).

The model for *L. cuprina* is most influenced by the seasonal variation in humidity and the magnitude of monthly rainfall (Fig. 7B). The species is predicted to occur along the east coast, and into the northern parts of South Africa, which are all regions that are known for their humidity. Adult blowflies are very dependent on moisture; and humidity is very important for egg development as blowfly eggs desiccate easily (Richards *et al*. 2009).

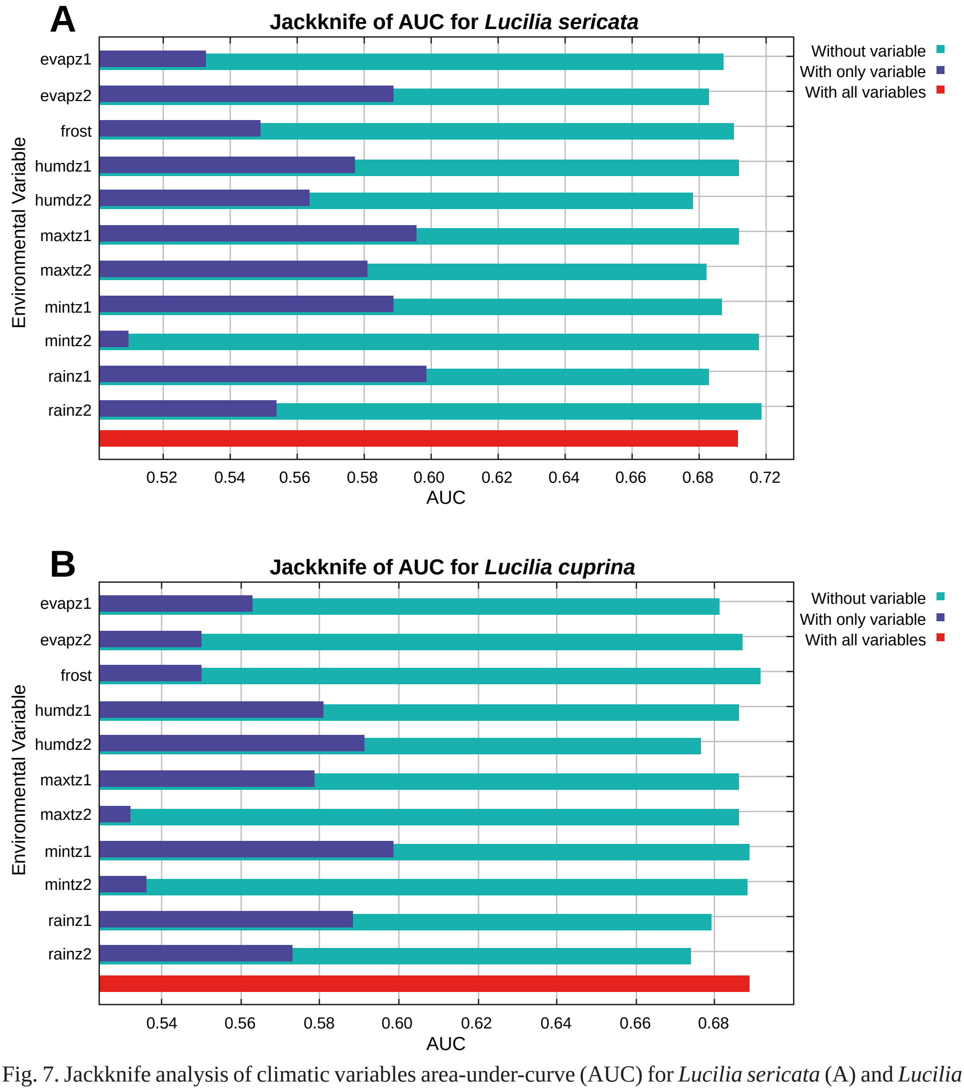

Fig. 7. Jackknife analysis of climatic variables area-under-curve (AUC) for *Lucilia sericata* (A) and *Lucilia cuprina* (B).

The models for both *L. sericata* and *L. cuprina* (Fig. 8) using the museum data and survey data separately, support the recommendations for focused surveys of areas for which there are very few records (Newbold 2010; Elith *et al*. 2011). Museum specimens are known to reflect bias in sampling effort and location and their use can influence the accuracy of predictive distribution models if no fieldwork is carried out to minimise the bias (Newbold 2010). The areas shown by the survey data to be suitable for these flies strongly correspond to the areas that were visited (Figs 1 & 8B & D). These data are biased due to the surveys, but when combined with the museum records, give a more complete depiction of whereabouts in the country these flies are likely to occur, as most of the climatically extreme areas of South Africa have been included. This must

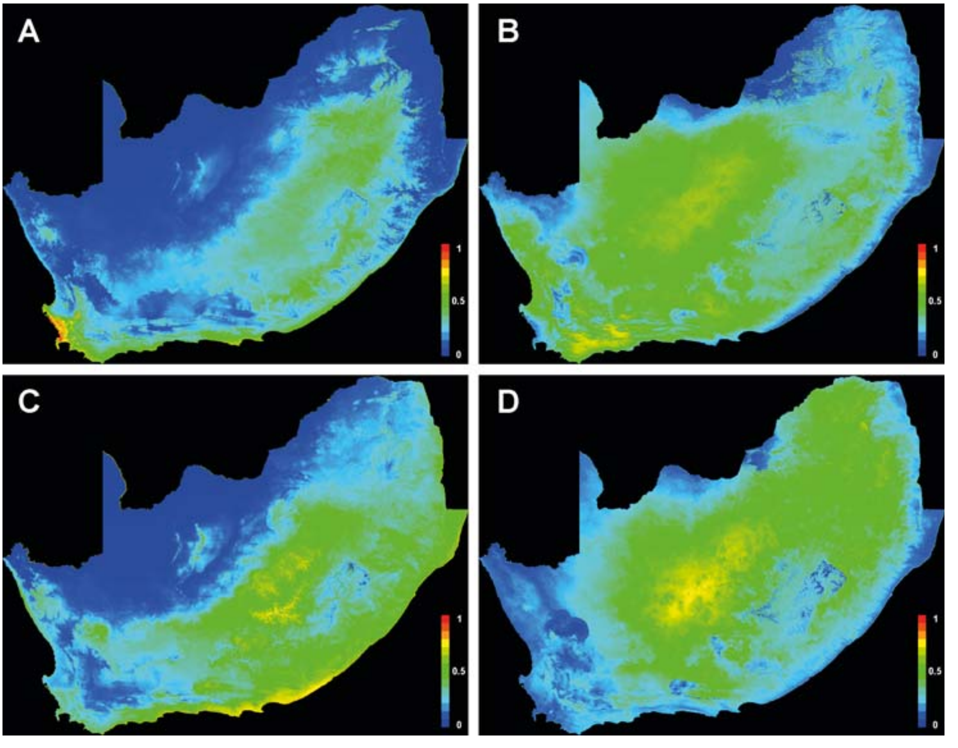

Fig. 8. Mean distribution maps for *Lucilia sericata* (A & B) and *Lucilia cuprina* (C & D) from museum (A & C) and survey (B & D) data only.

be considered when using modelling programmes to predict occurrences of species that may inhabit diverse climatic zones (Newbold 2010).

It has been reported that *L. sericata* is associated with areas inhabited by humans (Meskin 1986; Braack & de Vos 1987). However, the predicted occurrence of *L. sericata* shows no correlation with human population density, suggesting that this species is not an "urban" fly and occurs in both urban and rural environments. The potential distribution of *L. sericata* is also not correlated with wool production in South Africa, which is to be expected because this fly is not considered a pest in sheep-farming areas in South Africa (Hepburn 1943; Ullyett 1945; Vogt & Woodburn 1979).

L. cuprina has been thought to occur only in rural settings and not in areas populated by humans (Meskin 1986; Braack & de Vos 1987). The correlation between human population density and the predicted distribution of *L. cuprina* was not statistically significant, which supports this idea (Figs 4 and 6). *L. cuprina* has been a pest in sheep farming (Hepburn 1943; Ullyett 1945; Vogt & Woodburn 1979; Heath & Bishop 2006). The correlation between the areas in South Africa that have higher wool production (and therefore more sheep) and the predicted distribution of *L. cuprina* is not statistically significant (Figs 3 and 6). This is unexpected but may be explained by the fact that sheep farmers in South Africa are selecting breeds of sheep that do not have the skin fold around the anal area that promotes sheep strike, thereby eliminating the most common site of egg laying by this fly (A.R. Palmer pers. comm.).

L. sericata and *L. cuprina* appear to be largely generalists in that they are predicted to occur in most parts of South Africa, except in small areas of the south western and north eastern regions. This suggests that it is not possible to tell which species of *Lucilia* one is dealing with based only on geographic location. Morphological and molecular techniques are therefore advocated for identifying these two species, especially if they are being used in forensic investigations.

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