Predicting geographic distribution of seven forensically significant blowfly species (Diptera: Calliphoridae) in South Africa

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The predicted geographic distributions of seven forensically important blowfly species are modelled using the computer program Maxent, based on selected climatic variables for South Africa, a country with large climatic and environmental gradients. It is shown that although temperature was hypothesized to most influence the distributions of these ectotherms, moisture, and particularly humidity, was in fact usually paramount. *Chrysomya albiceps* (Wiedemann) and *C. marginalis* (Robineau-Desvoidy) had the most widespread geographic and climatic distribution, while the forest-associated *C. inclinata* (Walker) was the least widespread. *Chrysomya putoria* (Wiedemann) and *C. megacephala* (Fabricius) had very similar predicted distributions that were restricted mainly to Limpopo, Mpumalanga, KwaZulu-Natal and the coast of the Eastern Cape. *Chrysomya chloropyga* (Wiedemann) and *Calliphora croceipalpis* (Jaennicke) were the only species predicted to occur at high altitudes. Blowfly distributions restricted to part of the map area were predicted better than those that were more widespread in the region, presumably because species with extremely widespread distributions in a study area occupy nearly the whole range of variation of most predictor variables, leaving little variation with which the maximum entropy modelling method can discriminate between presence and absence of the organism.

Key words: Calliphoridae, climate variables, humidity, Maxent, predictive distribution, temperature.

INTRODUCTION

Numerous members of the family Calliphoridae (Diptera) are carrion-breeding flies that have veterinary, medical and forensic importance (Zumpt 1965). Some species are myiasis breeders (Baker *et al.* 1968; Hall *et al.* 2001), while others are known vectors of several enteric diseases (Sulaiman *et al.* 1988). Other carrion-breeding species may be used by forensic entomologists to detect the postmortem translocation of corpses (Smith 1986; Catts 1992). It is therefore valuable to know the geographic distribution of these flies to focus control measures and to improve our understanding of their forensic significance.

Because blowflies are ectotherms, temperature heavily influences their development, behaviour and physiology (Richards *et al.* 2009), but the influence of temperature on their geographic distribution is unknown. To test the hypothesis that temperature has a significant role in shaping blowflies' distributions, we predicted the known distribution of seven species using a suite of climatic variables and a maximum entropy technique implemented in the Maxent 3.0.2-BETA (July 2007) software (Phillips *et al.* 2006). Maxent is the only contemporary predictive biogeography program that provides an analysis of the degree of influence of each environmental layer on the predicted distribution. It is also one of only a few programs that do not need absence data to build a predictive model, and it has been advocated by several recent publications (Elith *et al.* 2006; Hernandez *et al.* 2006; Pearson *et al.* 2007).

South Africa was chosen as the study area for several reasons. First, the country has large environmental gradients, from tropical forest to desert, from coastal forest to montane grassland, and from summer to winter rainfall. This makes it highly likely that samples can be drawn from the entire environmental tolerance of the target species, which will greatly improve the performance of any predictive modelling technique (Vaughan & Ormerod 2003). Second, digital maps with a 1′ resolution (about 1.6 × 1.6 km) are available for a wide array of climatic variables (Schulze *et al.* 1997). Third, despite its climatic variability, the country is sufficiently small that any areas not

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represented by museum specimens can be surveyed relatively easily, resulting in levels of prevalence of occurrence records that have small standard errors for recommended measures of model performance (McPherson *et al.* 2004).

In this paper we present maps of the predicted distributions for seven species of carrion-associated Calliphoridae in South Africa made using Maxent, and comment on the climatic variables most influencing the predictions.

MATERIAL AND METHODS

Locality data

The species selected for modelling were *Chrysomya albiceps* (Wiedemann), *C. marginalis* (Robineau-Desvoidy), *C. megacephala* (Fabricius), *C. putoria* (Wiedemann), *C. chloropyga* (Wiedemann), *C. inclinata* (Walker), and *Calliphora croceipalpis* (Jaennicke). All of these species are indigenous except *C. megacephala,* which was first noted in South Africa about 20 years ago (Braack 1991). It is possible that *C. megacephala* has not yet spread to the limits of its ecological tolerance, which would violate some assumptions of predictive distribution modelling (Broennimann *et al.* 2007), providing an interesting case study. *Lucilia cuprina* (Wiedemann) and *L. sericata* (Meigen) were excluded because of taxonomic problems (Tourle *et al.* 2009), and *Chrysomya laxifrons* and *Calliphora vicina* was excluded because too few locality records were available.

Locality records were initially collected from three different sources: personal contacts (see Acknowledgements); literature searches (Baker *et al.* 1968; Paterson 1968; Braack & Retief 1986; Braack 1991; Louw & van der Linde 1993; Williams & Villet 2006); and museum records compiled from the collections of the South African Museum (Cape Town); Rhodes University (Grahamstown); Albany Museum (Grahamstown); Durban Natural Sciences Museum (Durban); Natal Museum (Pietermaritzburg); Kruger National Park Museum (Skukuza); and Onderstepoort Veterinary Institute (Pretoria). All of the museum material was re-identified due to advances in the recognition of species (Braack 1991; Wells *et al.* 2004; Rognes & Paterson 2005; Williams & Villet 2006; Tourle *et al.* 2009), and dubious literature records were ignored.

After collating these data, five field trips (see Fig. 1) were designed to collect data in otherwise poorly sampled areas and under-represented parts of the environmental gradients used in the models, following the recommendations of Vaughan & Ormerod (2003). Red-top® fly traps (Miller Methods, Ltd., Pretoria) were used to catch blowflies on all field trips. They were modified by attaching a half-litre jar containing 125 g of fresh chicken liver to the base of each trap. A gauze mesh was fastened across the mouth of the jar so that flies that were attracted into the trap by the odour of the liver could not become fouled in it, making them easier to handle and identify. One modified fly trap was set approximately every 50 km along the survey route and left for no fewer than four days. Blowflies were also collected from dead animals found along the roads between traps. Field trips were conducted in all seasons (see Fig. 1) except winter to optimize trapping and to ameliorate any possible seasonal trends (Braack & De Vos 1987).

The area between Ixopo (KwaZulu-Natal) and Sani Top border post (Lesotho) was chosen for a survey of altitudinal distribution for two reasons: it is one of the few places in South Africa with access to very high altitudes, and all species of interest potentially occur in this region. Four modified traps, placed approximately 300 m apart, were set at each of eight sites, separated by 300 m altitude, starting in Ixopo (900 m a.s.l.) and ending about 2 km west of Sani Top border post (3000 m a.s.l.) (Fig. 1), during January 2006. Traps were collected after five days and the contents were identified and counted.

Climatic variables

Eleven climatic predictor variables (Table 1) were selected to include fundamental climatic descriptors that are regarded as appropriate to ectotherms at global and regional scales (Mackey & Lindenmayer 2001; Robertson *et al.* 2003; Phillips 2008). Phillips *et al.* (2006) list three selection criteria that environmental data should meet when intended for modelling organisms' distributions. First, 'temporal correspondence should exist between occurrence localities and environmental variables'. Locality records used in our analyses were no older than 50 years, which is within the temporal precision of the climate variables used in this study (Schulze *et al.* 1997; Hijmans & Graham 2006). Second, 'the variables should affect the species' distribution at the relevant scales'. Since the species are generalist feeders that do not occur throughout the study area, it is likely that climate

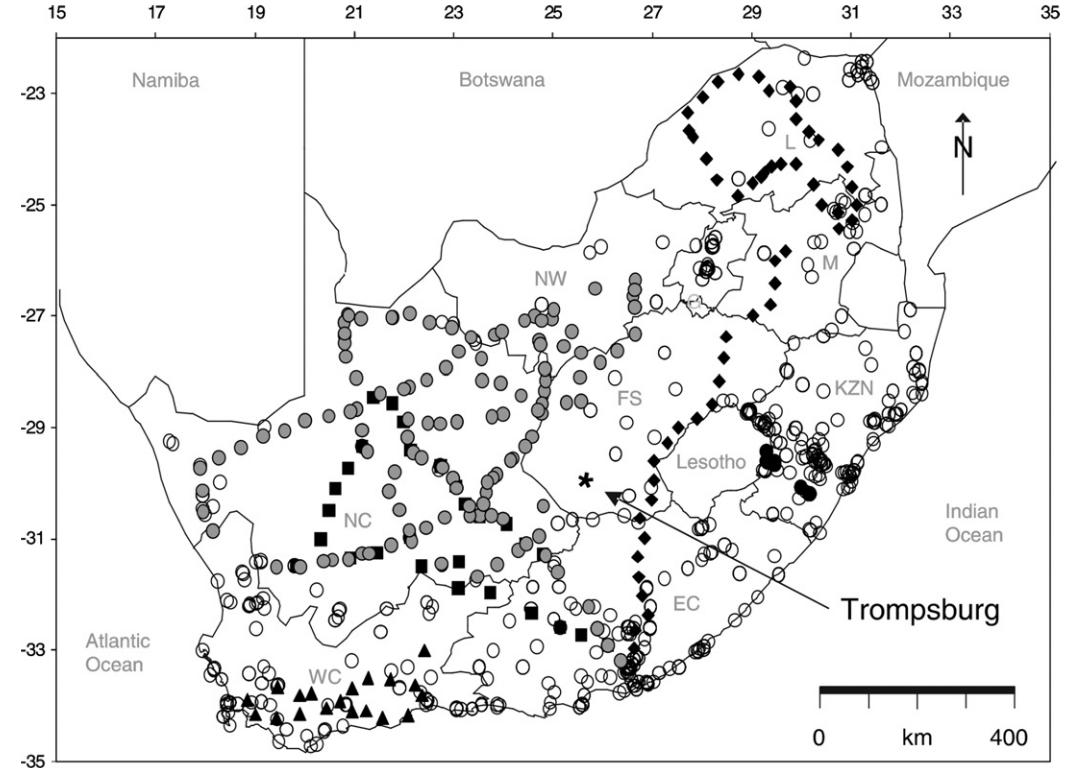

Fig. 1. Distribution of all locality records used in this study for all species tested. Data for individual species are presented in Fig. 2. Open symbols (❍) represent data obtained opportunistically from museums, literature and personal contacts; closed symbols represent targeted field trips as follows: ■, March 2002; ▲, October 2002; ●(grey), November 2005; ●, January 2006; ◆, January 2007. EC = Eastern Cape, FS = Free State, G = Gauteng, KZN = KwaZulu-Natal, L = Limpopo, M = Mpumalanga, NC = Northern Cape, NW = Northwest Province, WC = Western Cape, * = Trompsburg.

will shape their distributions at this spatial scale more than would food, breeding sites or other resources. Third, 'the choice of variables to use for modelling also affects the degree to which the model generalizes to regions outside the study area'. Because both the modelling area and the variation across each environmental gradient had been surveyed extensively across their extremes, this study was concerned with interpolation rather than extrapolation (*cf.* Phillips 2008), so this requirement is not violated.

Digital maps of the variables for South Africa were developed by Schulze *et al.* (1997) by interpolating from point data obtained from a network of weather stations distributed throughout South Africa and averaged over 10 years, to produce continuous digital maps (or 'layers') at a resolution of 60 pixels per degree (Schulze *et al.* 1997). Each climatic variable was originally represented by a map for each month, a total of 72 maps. To reduce the dimensionality of the climatic data set to rationalize computing effort, we performed principal component analyses (PCA) on the 12 monthly maps of each variable, and the factor scores for the first two principal components were kept, resulting in two summary layers for each variable (Table 1). The first variable (PCA axis 1) generally represented the magnitude of the climatic variable, while the second (PCA axis 2) generally represented seasonal variation in the same variable. The resulting layers were the same as those employed in predictive mapping by Robertson *et al.* (2001, 2003, 2004). For justification of data-reduction, see Vaughan & Ormerod (2003).

Statistical analysis

Apart from careful selection of the occurrence data and climatic predictor variables, thoughtful consideration has to be given to matching the modelling method to these data because some

Table 1. Climate variables used for building predicted geographic distribution maps.

Variables	Abbreviations	Predictor variable
Minimum temperature 1	Mint1	Component axis 1 (magnitude of minimum temperature) of a PCA of 12 digital surfaces of monthly minimum temperatures
Minimum temperature 2	Mint2	Component axis 2 (amplitude of minimum temperature fluctuations) of a PCA of 12 monthly minimum temperature surfaces
Maximum temperature 1	Maxt1	Component axis 1 (magnitude of maximum temperature) of a PCA of 12 monthly maximum temperature surfaces
Maximum temperature 2	Maxt2	Component axis 2 (amplitude of maximum temperature fluctuations) of a PCA of 12 monthly maximum temperature surfaces
Rainfall 1	Rain1	Component axis 1 (magnitude of rainfall) of a PCA of 12 monthly rainfall surfaces
Rainfall 2	Rain2	Component axis 2 (seasonal variation in rainfall) of a PCA of 12 monthly rainfall surfaces
Relative humidity 1	Humd1	Component axis 1 (magnitude of humidity) of a PCA of 12 monthly humidity surfaces
Relative humidity 2	Humd2	Component axis 2 (seasonal variation in humidity) of a PCA of 12 monthly humidity surfaces
Frost	Frost	Number of days with frost
Evaporation 1	Evap1	Component axis 1 (magnitude of evaporation) of a PCA of 12 monthly evaporation surfaces
Evaporation 2	Evap2	Component axis 2 (seasonal variation in evaporation) of a PCA of 12 monthly evaporation surfaces

models are especially suited to certain situations (Elith *et al.* 2006; Dormann *et al.* 2007). These situations include cases where biotic interactions such as competition, predation, parasitism or symbiosis affect the distribution of the target organism (Soberón & Phillips 2006; Phillips 2008). Fortunately, carrion-breeding blowflies are characteristically *r*-selected, weedy, and very mobile opportunists that are relatively unlikely to be affected by such interactions, so most predictive mapping models should be applicable to these species. If the occurrence data are sufficiently spatially remote from one another, there is less need to take spatial autocorrelation in account. We chose the Maxent v3.0.2-BETA software because it can work without absence observations, which are less reliable than presence data (Fielding & Bell 1997), and provides tools for diagnosing which predictor variables are contributing to the prediction. There are also publications giving useful guidance on fine-tuning Maxent analyses (*e.g.* Phillips & Dudík 2008).

Maxent estimates the probability distribution that is closest to uniform, or most spread out (of maximum entropy), subject to the constraint that the expected value of each environmental variable matches the average value for the set of locality records taken from the target distribution (Phillips *et al.* 2006). Default parameters of Maxent were employed for the regularization multiplier (1), maximum iterations (500), convergence threshold (0.00001) and maximum number of background points (10 000), with a logistic output type to construct the predictive distribution maps. Additionally, random seed analysis and a random test proportion of 20 %, instead of the default 0 %, were used. This meant that 20 % of all data points were reserved from building the predictive models and were instead used to measure predictive success. These data are termed 'test' data, while the data used to build the model are termed 'training' data (Pearson *et al.* 2007). Jackknife analyses and response curves (area under curve (AUC)) for each species were also constructed using Maxent. Detailed descriptions of these two analyses are appear in Pearson *et al.* (2007). The jackknife method is used to identify the most influential predictor variable(s) and to assess the predictive

Table 2. Numbers of locality records used to construct distribution maps for seven species of Calliphoridae.

Species	Number of training points	Number of test points	Total number of independent localities
C. albiceps	168	72	240
C. chloropyga	158	67	225
C. putoria	59	25	84
C. inclinata	24	9	33
C. marginalis	147	62	209
C. megacephala	24	9	33
Ca. croceipalpis	90	38	128

success of the model. This is achieved by removing one climatic variable and making a prediction from the remaining variables, and repeating this for each variable in turn. The change in fit of the prediction relative to that derived from the full data set is a measure of the influence of the omitted variable. Default Maxent jackknife procedures are performed on training data, test data and AUC values. Results in this paper focus on jackknife tests of AUC values only. The AUC is commonly used as a measure of models' overall performance with values commonly ranging from 0.50 (random) to 1.00 (perfect discrimination) (Hernandez *et al.* 2006). Values below 0.50 are considered to be worse than random and the predicted result is ignored. Other measures of predictive success are available (Fielding & Bell 1997), but AUC has been found to be robust to uneven prevalence in observations of occurrence that can produce artefacts in other performance measures (McPherson *et al.* 2004).

RESULTS AND DISCUSSION

Locality records

All geo-coordinates were rounded to the nearest minute so that the data were at the same resolution as the climatic maps, and duplicates of sites were weeded out in Maxent to avoid pseudo-replication. The final data set included a total of 952 species records from 653 different localities in South Africa (Fig. 1, Table 2). Observations of a particular species were separated by at least 2′ (*i.e.* 2 pixels or about 3.2 km), and often by 20–50 km, which is sufficient to make them statistically independent at the mapping precision (1′) and scale.

Climatic variables

Before computer-based predictive biogeography programmes were available, numerous authors (Smit & du Plessis 1926; Ullyett 1950; Zumpt 1956, 1965; Pont 1980; Prins 1982) made anecdotal statements about blowfly distribution without mention of any specific environmental variable. Because blowflies are ectotherms, temperature strongly influences their physiology and development (Higley & Haskell 2001; Ames & Turner 2003; Richards *et al.* 2009). It was therefore assumed that temperature would be the environmental variable most influencing geographic distribution of blowflies. However, the jackknife analyses indicate that the variables of least overall influence on blowfly distribution were maximum temperature, minimum temperature, and variation in humidity, with respective mean ranks of 7.9, 7.9 and 8.2 out of 11 (Table 3).

The jackknife analyses also indicated that for all species, frost risk and climate variables relating to aridity *e.g.* humidity and evaporation, had more influence on distribution than other variables (Table 3). More specifically, the amount of evaporation had a mean rank of 3.7 out of 11. The remaining climatic variables had larger standard deviations in rank than amount of humidity, indicating less consistency in their rank. These patterns became even more polarized if the analysis omitted *C. albiceps* and *C. marginalis*; these species had slightly atypical, relatively poorly fitted models for reasons discussed at the end of this paper.

Feeding behaviour of blowfly larvae in a carrion environment often results in maggots occupying a microhabitat saturated with moisture, and for this reason studies involving the immature stages of development mostly ignore moisture content, but authors often report ambient humidity for studies involving adult flies (Al-Misned 2001; Grassberger *et al.* 2003; Anderson 2004; Clark *et al.* 2006). Adult blowflies die more readily from even a brief absence of water than from extended cold temperatures

Table 3. AUC values for whole models and jackknife analyses for individual climate variables used to predict the distributions of seven species of Calliphoridae. AUC values indicate the quality of the predicted distribution map, while the Jackknifed models identify the environmental variable(s) most influential on the predicted distribution of each species. Values nearest to 1.00 represent a perfect validation; those near 0.5 represent a random fit. The predictor variables are arranged by mean rank across all species. Numbers in bold correspond to variables of most influence in a particular species while numbers in italics correspond to variables of least influence.

	Rank		AUC						
	Mean	S.E.	*C. albiceps*	*C. chloropyga*	*C. inclinata*	*C. marginalis*	*C. megacephala*	*C. putoria*	*Ca. croceipalpis*
Whole model									
Training data			0.76	0.83	0.98	0.84	0.95	0.90	0.92
Test data			0.62	0.78	0.97	0.59	0.77	0.85	0.86
Variables									
Evap1	3.7	1.9	0.54	0.72	0.77	0.56	**0.77**	0.71	**0.78**
Frost	4.0	1.7	0.49	0.67	**0.94**	0.59	0.74	0.76	0.70
Humd1	4.2	1.8	0.54	0.66	0.82	**0.60**	0.71	0.77	0.69
Maxt2	5.1	2.6	0.48	0.59	0.88	0.56	0.74	**0.80**	0.70
Mint2	5.4	2.4	0.53	0.71	0.79	0.52	0.74	0.63	0.74
Rain1	5.9	2.1	0.57	0.61	0.77	0.52	0.72	0.71	0.72
Rain2	6.5	2.1	0.52	**0.73**	0.79	0.55	0.52	0.69	0.69
Evap2	7.1	2.4	*0.46*	0.70	0.81	*0.51*	0.68	0.72	0.67
Maxt1	7.9	2.1	0.48	0.66	*0.68*	0.56	0.57	*0.61*	0.71
Mint1	7.9	2.3	0.52	*0.49*	0.72	0.59	0.53	0.71	*0.52*
Humd2	8.2	2.5	**0.58**	0.61	0.70	0.53	*0.43*	0.64	0.56

(6–9°C) (pers. obs.). Clearly, water loss is more influential than temperature. Humidity is also probably more of a limiting factor to egg development than temperature, as blowfly eggs desiccate easily and blowflies generally lay eggs on areas of a carcass that are very sheltered, especially crevices, body orifices and junctions between the ground and body (pers. obs.). These observations therefore support the primacy of moisture over temperature and offer two physiological mechanisms in different life stages to explain it.

Individual species' predictions

There is very little literature on the geographic distribution of these flies in South Africa and what is available is either anecdotal, fragmentary or outdated (Smit & du Plessis 1926; Ullyett 1950; Zumpt 1956, 1965; Pont 1980; Prins 1982). Most recently, Williams & Villet (2006) provided a detailed account of locality records for two invasive calliphorids, *C. megacephala* (F.) and *Calliphora vicina* (Meigen), but it accounts for only two species and provides limited insight into their potential geographic distribution. Our predictions provide both detailed predictive distribution maps and insight into the biology seven South African blowfly species.

Chrysomya albiceps. This species has a very wide climatic and predicted geographic distribution and can probably be found in all parts of South Africa except at very high altitudes (Figs 2, 3). The results from the altitude survey support these findings and imply that the species may occur only as high as 2400 m but are most common below 1800 m (Fig. 3). The species is distributed widely in Africa and Europe (Zumpt 1965; Pont 1980). Jackknife analyses show that no single climatic variable could be identified as significantly influential on the geographic distribution because jackknife analysis

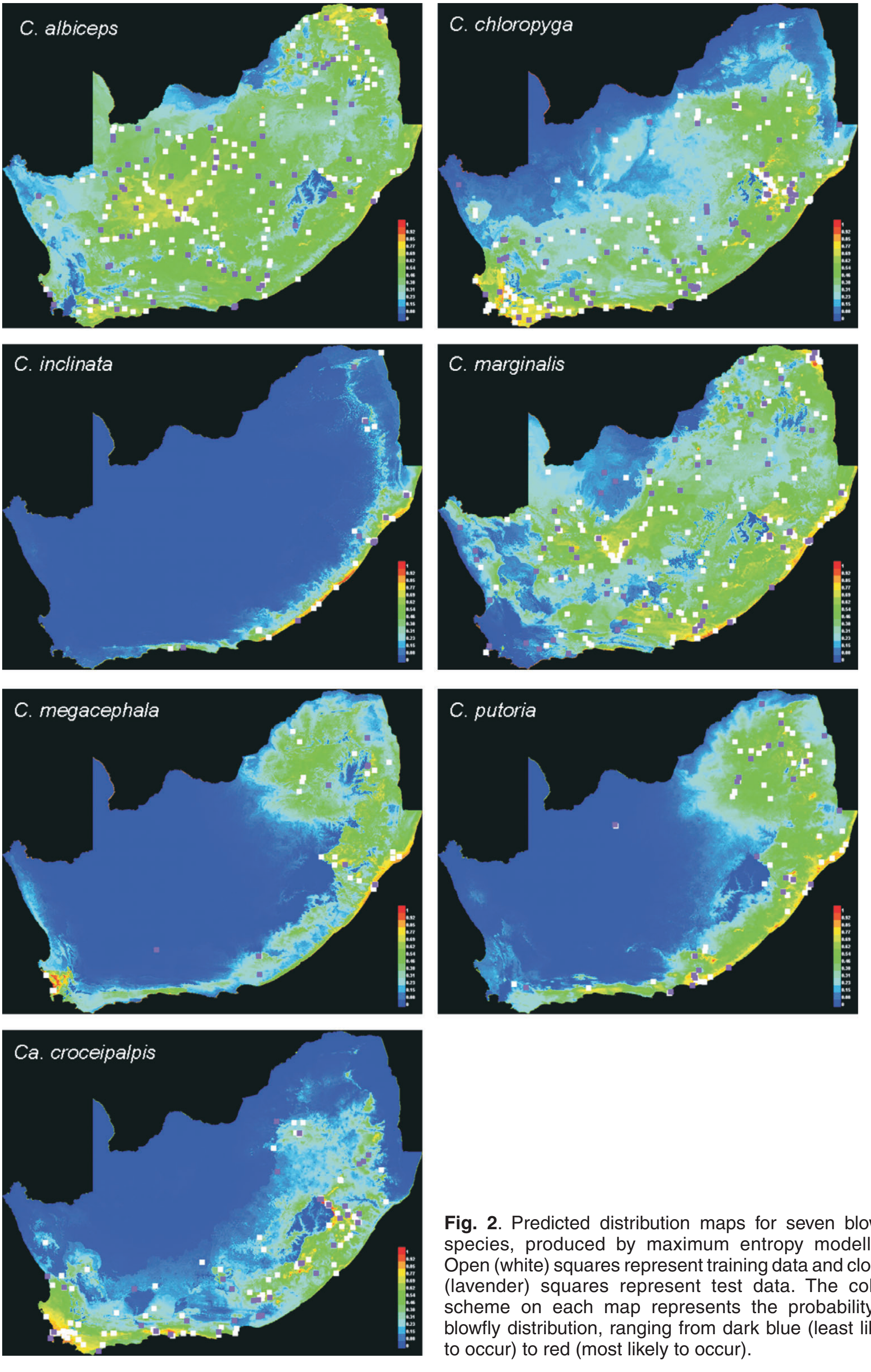

Fig. 2. Predicted distribution maps for seven blowfly species, produced by maximum entropy modelling. Open (white) squares represent training data and closed (lavender) squares represent test data. The colour scheme on each map represents the probability of blowfly distribution, ranging from dark blue (least likely to occur) to red (most likely to occur).

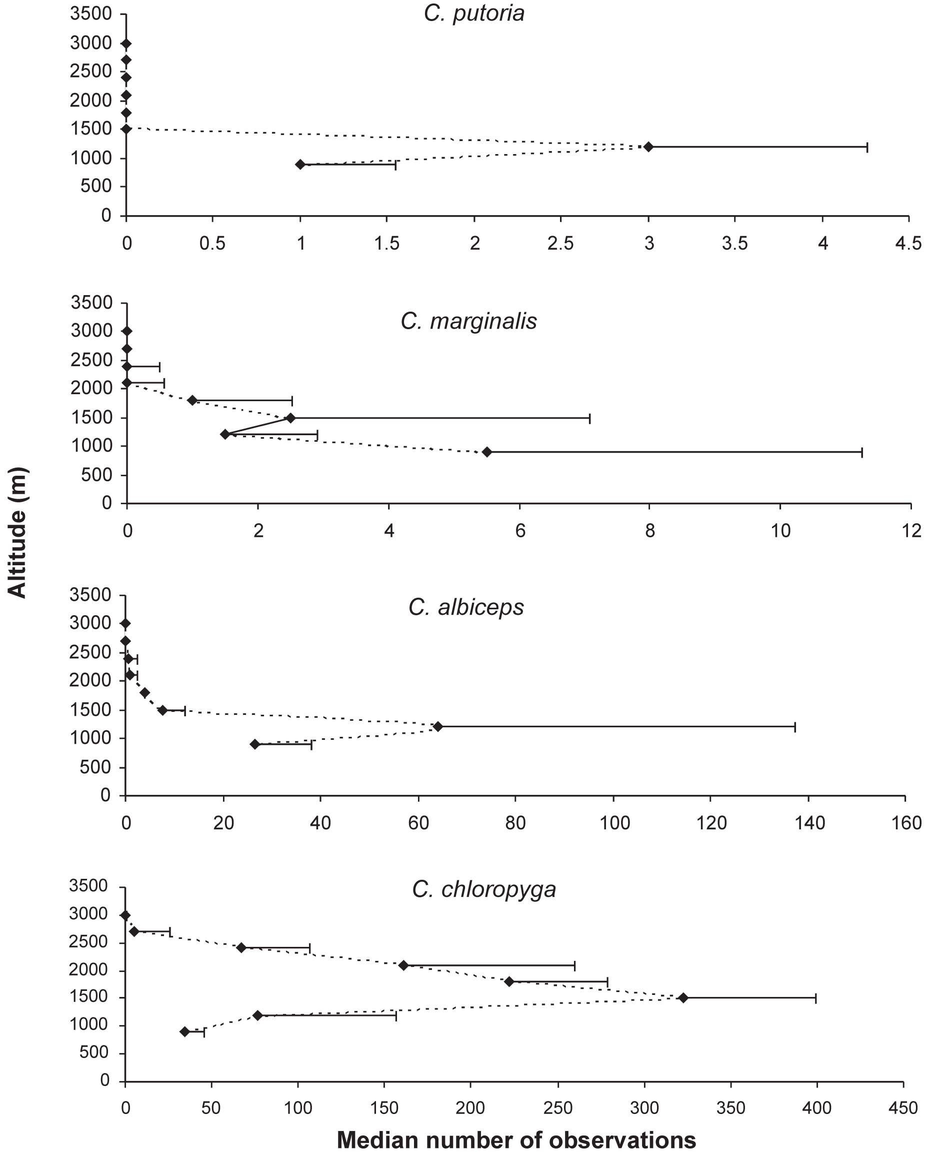

Fig. 3. Abundance of four species of blowfly trapped at different altitudes between Ixopo and Sani Top, KwaZulu-Natal, in January 2007.

values for all climate variables were between 0.46 and 0.58 (Table 3). Together with this, seven of the 11 variables yielded an AUC value within 0.06 of one another.

Chrysomya marginalis. This species had a very similar result to that of *C. albiceps* (Figs 2, 3; Table 3), and seven of the 11 variables yielded an AUC value within 0.06 of one another. It is also widespread in Africa (Zumpt 1965; Pont 1980), suggesting that it has wide climatic tolerances, although its physiological tolerance to extreme temperatures is not unusual for its genus (Richards *et al.* 2009).

Chrysomya putoria. This species has a tropical distribution throughout central, eastern and southern Africa (Table 4) and the Neotropics (Guimarães *et al.* 1978; Baumgartner & Greenberg 1984; Laurence 1981, 1988; Wells *et al.* 2004; Rognes & Paterson 2005). It was introduced into southern Brazil during the 1970s (Guimaríes *et al.* 1978) and

Table 4. Locality records of *Chrysomya putoria* in Africa, excluding South Africa.

Country	Collection/reference
Botswana	Albany Museum, Rhodes University, Paterson (1968), Rognes & Paterson (2005)
Cameroon	Natal Museum, Paterson (1968), Rognes & Paterson (2005)
Democratic Republic of Congo	Paterson (1968), Rognes & Paterson (2005)
Eritrea	Paterson (1968)
Ethiopia	Zumpt (1965)
Gambia	Natal Museum, Rognes & Paterson (2005)
Ghana	Natal Museum, Paterson (1968), Rognes & Paterson (2005)
Kenya	Natal Museum, Rhodes University, Rognes & Paterson (2005)
Liberia	Paterson (1968), Laurence (1988)
Madagascar	Natal Museum, Rognes & Paterson (2005)
Malawi	Natal Museum
Mauritius	Natal Museum, Rognes & Paterson (2005)
Mozambique	South African Museum, Paterson (1968)
Namibia	South African Museum, Kurahashi & Kirk-Spriggs (2006)
Nigeria	Paterson (1968)
Senegal	Paterson (1968), Rognes & Paterson (2005)
Sierra Leone	Paterson (1968), Rognes & Paterson (2005)
Sudan	Paterson (1968)
Swaziland	Rognes & Paterson (2005)
Tanzania	Laurence (1988), Paterson (1968), Rognes & Paterson (2005)
Uganda	Natal Museum, Rognes & Paterson (2005)
Zambia	Albany Museum, Rhodes University, Rognes & Paterson (2005)
Zimbabwe	Albany Museum, Natal Museum, Rhodes University

has since spread north through the tropical regions of South and Central America (Wells *et al.* 2004; Rognes & Paterson 2005). The predicted distribution of *C. putoria* in South Africa is mainly along the eastern coast of South Africa, Mpumalanga and the central parts of Limpopo (Fig. 2). The specimen from Kuruman (Northern Cape) appears to be outside the normal geographical range of the species, but it was caught by professional dipterists (J. Londt and A. Whittington) and we saw no reason to exclude it from the model; it seems to have had little effect on the prediction. Few specimens were recorded in the altitude survey (Fig. 3), suggesting that this species prefers areas below 1200 m. The jackknife analyses suggest that the climate conditions that most influenced the distribution of *C. putoria* are higher humidity and lower variation in maximum temperature (Table 3). These two variables describe a moist, stable environment that is characteristic of tropical environments and therefore validates its common name of 'tropical latrine blowfly'. The Drakensberg mountain range appears to act as a natural barrier to the inland spread of *C. putoria,* probably because it plays a major role in creating a rain shadow in the interior of South Africa.

Chrysomya megacephala. This species is also a latrine fly, and is widely distributed in the Oriental and Australasian regions (Bohart & Gressitt 1951; Wijesundara 1957; Zumpt 1965; Khole 1979; Levot *et al.* 1979; O'Flynn 1983; Nishida 1984; Nishida *et al.* 1986; Wells & Kurahashi 1994). It was first noted in South Africa in 1971 (Braack 1991; Williams & Villet 2006). This raises the issue of whether a meaningful model can be built for this species, because it may not have spread to the limits of its environmental tolerance in the intervening 38 years, leading to under-prediction of its true distribution (Broennimann *et al.* 2007). Indigenous South African blowflies can disperse 37–63 km per generation in (Braack & Retief 1986; Braack & de Vos 1990), and can produce 10–20 generations a year. If *C. megacephala* is comparable, it could potentially spread over 3000 km in ten years, as it in fact did when it was introduced to South America (Laurence 1981, 1986). It is likely that *C. megacephala* was introduced to South Africa *via* several entry ports (Braack 1991; Williams & Villet 2006), which, combined with its likely dispersal ability, suggests that it has probably

Table 5. Locality records of *Chrysomya megacephala* in Africa, excluding South Africa.

Country	Locality	Date	Collector	Collection
Côte d'Ivoire	Abidjan	21 April 1989	J.G.H. Londt	Natal Museum
Kenya	Sigor	31 Jan 1973	I. Bampton	Natal Museum
Zimbabwe	Harare	12 Dec 2000	N. Lunt	Rhodes University
Zambia	Kitwe	18 July 2001	N. Mkize	Rhodes University

saturated its potential distribution.

Zumpt (1965) noted that the distribution of *C. megacephala* in Australia extended along much of the east coast, as far south as Bateman's Bay (35°43′S 150°10′E), but was not recorded at any distance from the coast. In South Africa the species potentially occurs along the coast from the Western Cape to KwaZulu-Natal, and in Mpumalanga, Limpopo and the northern Free State (Fig. 2). Its distribution in the rest of Africa is not well documented (Braack 1991; Gabre *et al.* 2005; Williams & Villet 2006), while Zumpt (1965) and Pont (1980) mention records on islands off the east coast of Africa, including Madagascar, Réunion and Mauritius. There are only four other African locality records, from four different countries (Table 5). *Chrysomya megacephala* was not trapped in the altitudinal survey, but it was found from sea level to over 1400 m a.s.l. in the Drakensberg by other collectors. Higher environmental moisture and stable temperatures most influenced the geographic distribution (Table 3), describing a more-or-less tropical species.

Chrysomya inclinata. This fly inhabits dense tickets and forest-like vegetation, which is strongly reflected in its predicted distribution. It is unlikely to occur in Free State, Gauteng, Northern Cape and North West Province (Fig. 2), which are characteristically more arid provinces (Schulze *et al.* 1997). The predicted distribution is primarily coastal in the Western Cape, Eastern Cape and KwaZulu-Natal, and continues through Mozambique to Ethiopia (Zumpt 1965). In Mpumalanga and Limpopo the species is predicted to occur along the escarpment and in other forested areas like the Soutpansberg. The geographic distribution of *C. inclinata* was most influenced by low frost risk, higher environmental moisture and stable maximum temperature, but several other variables also make important contributions to the prediction (Table 3), which may be a reflection of the apparently stenotopic niche of this species.

Chrysomya chloropyga. This species more widely distributed in South Africa than its sister species, *C. putoria*, occurring throughout Gauteng, Mpumalanga, KwaZulu-Natal, Eastern Cape, Western Cape, most of Northwest Province and Free State, and parts of Northern Cape and Limpopo (Fig. 2). *Chrysomya chloropyga* was the only species captured at all altitudes in the altitudinal survey and was the most common species at altitudes above 2400 m (Fig. 3). Jackknife analysis showed that low evaporation and low variability of both rainfall and evaporation were variables that strongly influenced the prediction (Table 3), indicating a susceptibility to desiccation. Its physiological tolerances appear to be adapted to more temperate temperatures than other southern African blowflies (Richards *et al.* 2009).

Calliphora croceipalpis. This blowfly is prevalent throughout Gauteng, Eastern Cape and Western Cape, and largely absent from Northern Cape, Northwest Province, Limpopo, Mpumalanga, and Free State (Fig. 2). Its distribution continues *via* East Africa to Ethiopia and Yemen (Zumpt 1965; Pont 1980). Zumpt (1965) states that *Ca. croceipalpis* 'is a common fly in South Africa, but in tropical parts is probably restricted to higher altitudes'. The predicted distribution of *Ca. croceipalpis* is primarily linked to low evaporation (Table 3). The prediction is also linked to low variation in minimum temperatures (Table 3); *Ca. croceipalpis* is a cold-adapted species (Richards *et al.* 2009) and 62 % of South African collecting records were gathered in the four months from July to October. Prins (1982) reported that this species is 'more active during the winter months and early spring'. This may account for its tendency to be associated with high-lying ground (Fig. 2) (as opposed to simply higher altitudes; *cf.* Zumpt 1965), especially outside the Western Cape, but might also be a pre-adaptation to avoiding interspecific competition (Soberón & Peterson 2005) because its relatives are adapted to Holarctic climates.

Clearly, not all blowflies occur throughout the country, which may be significant to medical, veterinary and forensic entomologists. For instance, control measures against pestilent blowflies can be targeted at the full area of occurrence and not squandered elsewhere. If larvae of *C. putoria* were found on a corpse in *e.g.* Trompsburg (which has never been surveyed for blowflies (Fig. 1), but is predicted to be free of *C. putoria* (Fig. 2)), this would be reason to suspect that the corpse had been tampered with or relocated from a site where *C. putoria* is predicted to occur (Smith 1986; Catts 1992). Predictive maps can also be used to reconstruct the community of carrion insects that could be expected to occur at sites like Trompsburg for which no faunal data are available, which may be important in applying succession matrix models to estimating a postmortem interval (Lamotte & Wells 2000).

Predictive success of Maxent

We note that Maxent performs better for some species than for others (Table 3). *Chrysomya albiceps* and *C. marginalis* were shown to have widespread distributions in the study area, and therefore occupy nearly the whole range of most predictor variables. It is likely that this has led to the situation illustrated by Vaughan & Ormerod (2003: fig. 1b), where parts of an environmental gradient that are relevant to the distribution of a species do not occur within the geographical area under study, and are therefore not considered in the modelling process. This seems to have challenged the predictive power of the maximum entropy modelling method as both species had the two lowest AUC values for training and test data (Table 3). Species with a localized geographic distribution had the highest AUC value for both training and test data, implying nearly perfect models. It seems that Maxent, and probably most predictive mapping methods, is most capable in predicting geographic distribution for species with limited climatic distributions and that prediction for species with widespread climatic distributions are less successful. These conclusions support the findings of other studies (Stockwell & Peterson 2002; Segurado & Araujo 2004; Hernandez *et al.* 2006; McPherson & Jetz 2007; Pearson *et al.* 2007).

Stockwell & Peterson (2002) and Hernandez *et al.* (2006) explain that different habitat preferences of sub-populations within a species of widespread geographic and climatic distribution exist as a distinct climatic range and that when the species is modelled as a whole, the resulting distribution is an overestimate of the species' realized niche. This results in the prediction appearing more random. Therefore, adaptation by local populations to surrounding environments may decrease the accuracy of the predictive model. Evidence of such local adaptation has been found in the developmental ecology of *C. albiceps* (Richards *et al.* 2008), lending support to this explanation.

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