

## COMPARING CLIMATE AND VEGETATION AS LIMITING FACTORS FOR SPECIES RANGES OF AFRICAN TICKS

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**Abstract.** The broad-scale factors that limit the species ranges of ticks have not been definitively established. I used environmental data covering the whole of mainland Africa and a database of 34 063 published locality records for African ticks to assess the importance of different environmental variables as limiting factors for tick species ranges. The abilities of categorical and continuous variables (including rainfall, temperature, vegetation type, a  $6 \times 6$  degree grid, political regions, and Normalized Difference Vegetation Index [NDVI]) to predict tick distributions were established using a new set of methods where logistic regression equations based on different variables for each of 50 tick species are compared.

The results show that, on average, climatic variables are better predictors of tick distributions than vegetation-related variables. Given also that most tick distributions are not limited by those of their host species, it can be inferred that the primary factor preventing the expansion of tick species ranges is the direct effect of climate. Minimum temperature, maximum temperature, and rainfall are of similar predictive ability; when considered together, their predictive ability increases substantially. I conclude that the key to describing tick distributions is the covariance of temperature and rainfall. Attempts at tick eradication are unlikely to be successful unless suitably broad areas are targeted, but the close relationship between tick distributions and climate should make the prediction of tick-borne disease outbreaks relatively easy.

**Key words:** Africa; biogeography; broad-scale ecology; epidemiology; Ixodidae; landscape ecology; limiting factors; logistic regression; parasitology; spatial ecology; spatial modeling; ROC plot; ticks.

### INTRODUCTION

The study of ecology relies heavily on the description of associations between particular species and the habitats in which they occur. Habitat preference may be apparent at a variety of different scales. While some environmental variables cause heterogeneity in the distribution of organisms on a scale of meters or kilometers, others act over much larger areas; broad-scale habitat requirements frequently take precedence over those that are relevant at smaller scales (Wu and Loucks 1995). In this paper I use correlations between species ranges and variables acting at similarly broad scales to explore the relationship between species occurrence and habitat type, and to generate hypotheses about ecological relationships at smaller scales.

Numerous previous studies have used multivariate analyses to generate predictive equations, estimate the likely occurrence of particular species in a spatially explicit manner, and make inferences about the importance of different environmental variables as determinants of their distributions (e.g., Osborne and Tigar

1992, Rogers and Randolph 1993, Austin et al. 1996, Rogers et al. 1996, Robinson et al. 1997, Lindenmayer et al. 1999). These studies are heavily reliant on the optimization of predictive linear equations for individual species and interpretation of the coefficients associated with the predictor variables. While this approach is useful for answering certain kinds of questions, its value is limited by the problem that the values of the coefficients are affected by collinearity and spatial autocorrelation (Legendre 1993).

I outline a conceptually different approach to the same problem, using robust comparisons between (as opposed to within) equations to determine which variables are the most important broad-scale determinants of tick species ranges, and develop a method for comparing the predictive abilities of categorical and continuous environmental variables. Comparisons are performed in such a way that neither autocorrelation nor collinearity among the predictor variables affects the results. The methods are illustrated using data for 50 species of African tick.

Despite the economic importance of ticks (Acari: Ixodidae) as vectors of livestock and human pathogens (Hewetson 1981), the broad-scale ecology of only a few species has been studied in any detail (e.g., Lessard et al. 1990, Randolph 1993, Randolph and Rogers 1997; Toomer, *unpublished manuscript*). Work focusing mainly on the brown ear tick *Rhipicephalus ap-*

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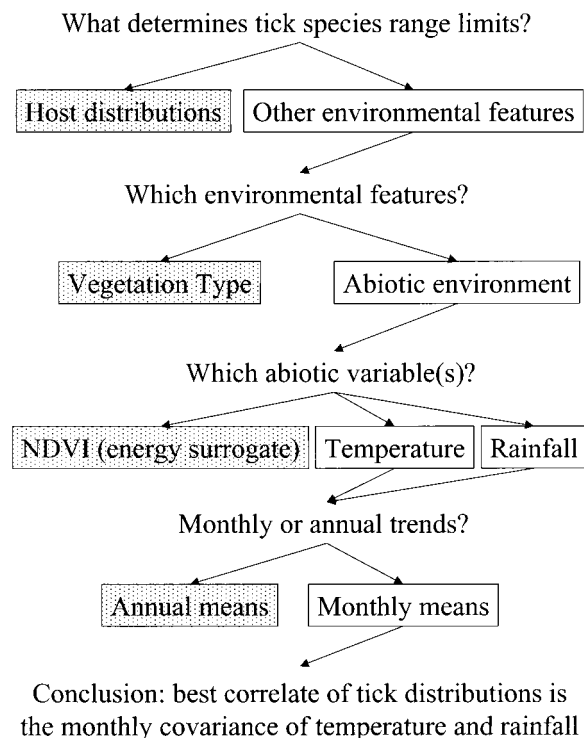


FIG. 1. Logic tree showing the alternative hypotheses considered at each stage of the analysis. After posing each question, different alternatives were considered (indicated by arrows), and the most likely was then pursued further. Shaded boxes indicate "blind alley" variables that were removed from contention. The first step, elimination of the host distributions hypothesis, is dealt with elsewhere (Cumming 1998, 1999a). The tree does not include the additional analysis that was necessary at the second stage to test the effects of categorization on model accuracy.

*pendiculatus* Neumann, an economically important pest of livestock in East and Southern Africa, has shown the potential value of climatic variables as correlates of tick mortality rates (Randolph 1994, Randolph and Rogers 1997) and species ranges (e.g., Lessard et al. 1990, Rogers and Randolph 1993; Toomer, unpublished manuscript). The general applicability of

these pioneering studies is tested using data for 50 African tick species (roughly one fifth of the ~240 described African species).

The variables that have been proposed as possible limiting factors for ticks include host availability (e.g., Hoogstraal and Aeschlimann 1982, Norval et al. 1994; also cf. Klompen et al. 1996), vegetation type and structure (e.g., Tukahirwa 1976, Norval 1977, Minshull and Norval 1982), climate (e.g., Walker 1974, Randolph 1994), and elevation (Walker 1974). While these variables are all closely interrelated, both statistically and biologically, their relative importances differ. Most of the African ticks for which reasonable numbers of collection records exist do not show high levels of host specificity, and few (if any) of these species can be considered host-limited (Cumming 1998, 1999a). I consider each of the following variables as potentially limiting factors (or correlates of such factors) for the species ranges of African ticks: vegetation type, plant productivity, elevation, maximum temperature, minimum temperature, and rainfall. Taken in the context of previous work, the results suggest that the species ranges of ticks in Africa are largely determined by the direct effects of climate.

#### MATERIALS AND METHODS

##### Overview of model development and model assessment

Logistic regression models were used to establish broad-scale correlations between different sets of variables and the distributions of ticks. The main assumption which drove the analysis was that when all other quantities are equal (i.e., the data are for the same species, of comparable type, at the same extent and grain, and the same modeling technique is used), the variable or variable set which produces the better fitting equation is the better predictor of the tick's distribution, and hence is the more likely limiting factor. The reasoning behind this assumption is best illustrated by a simple example: Imagine that your kitchen ceiling has developed a small, damp patch that is becoming moldy. The dampness is confined to a single spot, so you hardly

TABLE 1. Summary of main logistic regression models compared during the analysis.

Data type	Variable classes considered	Number of variables and models
Categorical	categorized climatic data, vegetation type, political regions, $6 \times 6$ -degree grid	differing numbers of predictors selected from ~80 categories <sup>†</sup> in each regression; $4 \times 50$ logistic regression models
Continuous	mean monthly data for rainfall, minimum and maximum temperature, and NDVI	12 variables in each regression; $4 \times 50$ logistic regression models
Continuous	mean annual data for rainfall, minimum and maximum temperature, NDVI, and elevation.	one variable in each regression; $5 \times 50$ logistic regression models

Note: Each set of comparisons was performed for the full range of 50 different tick species.

<sup>†</sup> Categorical data are modeled using "dummy" 1–10 variables. In each regression, only categories containing data points have nonzero coefficients; therefore, the number of variables used in any equation is proportional to the spatial scatter of the data, and hence to sample size.

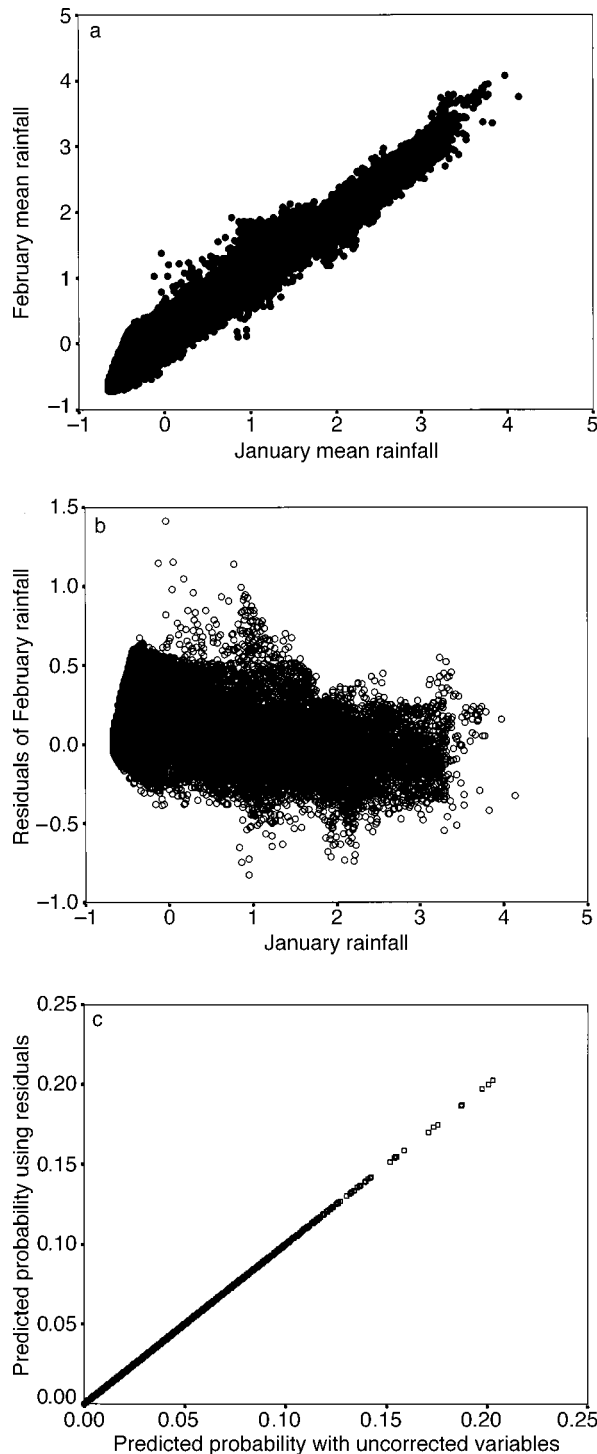


FIG. 2. Demonstration of the lack of effect of removing collinearity on the predictions obtained from a logistic regression model. (a) January and February rainfall across Africa are highly collinear, with  $r^2 = 0.976$  (each point on the plot represents standardized data for a single locality). (b) The collinearity can be removed by using the residuals of the regression of February rainfall on January rainfall in place of February rainfall itself. (c) The probabilities obtained by logistic regression for the likelihood of occurrence of *Amblyomma hebraeum* at each point are identical for models

contemplate the idea that a recent repainting is responsible. It is partially over the kitchen sink, leading to your next correlative hypothesis, but the area does not match the area that might receive excess humidity. Finally, you enter the roof and notice that there is a missing tile immediately over the damp patch. The match of size, position, and shape is good enough to convince you that the mold is caused by a leak in your roof. At each stage of this investigation, the conclusions are based on the correlation between an observed distribution (that of mold) and the distribution of potential determining factors in the local environment. In the same way, the match of the spatial distribution of environmental factors to the spatial distribution of animals can be used as a basis for erecting hypotheses that later experiments (fixing the roof) can support or refute. The results demonstrate correlation rather than causation, and while they provide an objective basis from which to think about the relative importances of different broad-scale factors, they should ideally be verified using controlled experiments at smaller scales.

Correlations between animal distributions and the distribution of environmental variables are complicated by covariance. The relative timing of a rainfall event, for example, may be as important as its magnitude; many animals can survive warm, wet weather, but not cold, wet weather. The covariance problem and the binary nature of collection records dictate the use of a multivariate logistic method.

The methods were also constrained by available data. While good interpolated climatic and remotely sensed data sets were available, giving quantitative estimates at relatively fine grains over the whole African continent, the same was not true for vegetation type. The process of model development can be thought of as following a logical decision tree (Fig. 1): Having identified several competing hypotheses, the first step was to eliminate the possibility that tick distributions are limited by their hosts (Cumming 1998, 1999a). In this paper I consider the remaining hypotheses, and start by comparing the correlations of vegetation and climate with tick distributions. This comparison required the categorization of climatic data, since vegetation type was only available in the (weaker) categorical form. I also included a regularly shaped grid (as a null model) and political boundaries (because of the country-by-country nature of the data) in the categorical comparison. The predictive ability of these variables was assessed by building predictive logistic regression models for each of 50 tick species,

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using the noncollinear residual of February rainfall and January rainfall (y-axis), or the collinear data for February rainfall and January rainfall (x-axis); the slope of this line is unity. Because AUC values are obtained from the presence/absence data and the predicted probabilities generated for each cell by the logistic regression, correcting for collinearity has no effect on the AUC.

TABLE 2. Areas Under the Curves (AUCs) from different models for each of the 50 tick species considered in the analyses.

Tick species (n)	Climate	Veg	Grid6	Politic	Clim-37	Mrfall	Mmint	Mmaxt	NDVI
<i>Amblyomma cohaerens</i> (211)	0.888	0.841	0.752	0.809	0.968	0.893	0.924	0.926	0.873
<i>Amblyomma gemma</i> (375)	0.862	0.863	0.789	0.865	0.982	0.936	0.930	0.927	0.775
<i>Amblyomma hebraeum</i> (503)	0.799	0.835	0.873	0.797	0.983	0.916	0.949	0.954	0.875
<i>Amblyomma lepidum</i> (319)	0.860	0.880	0.797	0.852	0.950	0.910	0.867	0.850	0.701
<i>Amblyomma marmoreum</i> (134)	0.779	0.840	0.791	0.843	0.933	0.787	0.903	0.902	0.781
<i>Amblyomma nuttalli</i> (146)	0.777	0.718	0.725	0.741	0.884	0.798	0.846	0.797	0.730
<i>Amblyomma pomposum</i> (134)	0.800	0.770	0.745	0.822	0.966	0.957	0.938	0.903	0.906
<i>Amblyomma rhinocerotis</i> (119)	0.836	0.757	0.808	0.823	0.954	0.861	0.881	0.893	0.720
<i>Amblyomma sparsum</i> (197)	0.885	0.843	0.837	0.869	0.951	0.891	0.905	0.870	0.771
<i>Amblyomma tholloni</i> (256)	0.787	0.720	0.726	0.764	0.908	0.840	0.863	0.832	0.809
<i>Amblyomma variegatum</i> (1639)	0.834	0.746	0.816	0.842	0.895	0.866	0.807	0.807	0.628
<i>Aponomma exornatum</i> (184)	0.789	0.776	0.761	0.753	0.880	0.818	0.828	0.788	0.711
<i>Aponomma latum</i> (184)	0.782	0.761	0.764	0.750	0.871	0.809	0.820	0.776	0.779
<i>Argas persicus</i> (176)	0.715	0.714	0.728	0.735	0.717	0.627	0.620	0.644	0.574
<i>Boophilus annulatus</i> (226)	0.789	0.794	0.800	0.835	0.907	0.838	0.838	0.848	0.813
<i>Boophilus decoloratus</i> (1965)	0.844	0.799	0.835	0.840	0.881	0.780	0.822	0.837	0.716
<i>Boophilus geigy</i> (135)	0.721	0.698	0.844	0.806	0.985	0.955	0.940	0.968	0.880
<i>Boophilus microplus</i> (296)	0.834	0.774	0.782	0.870	0.969	0.925	0.916	0.931	0.871
<i>Dermacentor rhinocerus</i> (151)	0.852	0.830	0.820	0.840	0.935	0.837	0.863	0.842	0.727
<i>Haemaphysalis aciculifer</i> (168)	0.834	0.797	0.777	0.765	0.924	0.852	0.875	0.865	0.765
<i>Haemaphysalis leachi</i> (1002)	0.842	0.829	0.818	0.824	0.874	0.756	0.846	0.836	0.666
<i>Haemaphysalis parvula</i> (147)	0.779	0.788	0.731	0.768	0.941	0.908	0.874	0.878	0.791
<i>Haemaphysalis spinulosa</i> (159)	0.793	0.753	0.750	0.722	0.860	0.810	0.811	0.814	0.793
<i>Hyalomma albiparvum</i> (256)	0.866	0.742	0.739	0.841	0.995	0.973	0.982	0.981	0.888
<i>Hyalomma dromedarii</i> (231)	0.769	0.753	0.784	0.757	0.870	0.795	0.740	0.779	0.617
<i>Hyalomma impetatum</i> (304)	0.786	0.792	0.775	0.735	0.862	0.795	0.768	0.765	0.658
<i>Hyalomma rufipes</i> (1122)	0.840	0.831	0.813	0.857	0.882	0.663	0.802	0.816	0.726
<i>Hyalomma truncatum</i> (1468)	0.817	0.826	0.795	0.828	0.868	0.705	0.803	0.826	0.710
<i>Ixodes cavipalpus</i> (165)	0.812	0.823	0.758	0.843	0.957	0.915	0.924	0.926	0.892
<i>Ixodes pilosus</i> (112)	0.839	0.885	0.820	0.802	0.991	0.824	0.970	0.961	0.824
<i>Margaropus winthemi</i> (95)	0.807	0.765	0.867	0.748	0.991	0.862	0.983	0.988	0.819
<i>Ornithodoros moubata</i> (223)	0.842	0.833	0.792	0.852	0.880	0.811	0.854	0.837	0.743
<i>Otobius megnini</i> (320)	0.847	0.895	0.875	0.894	0.987	0.842	0.984	0.984	0.794
<i>Rhipicephalus appendiculatus</i> (1258)	0.886	0.842	0.817	0.861	0.942	0.880	0.897	0.876	0.799
<i>Rhipicephalus capensis</i> (349)	0.882	0.897	0.885	0.898	0.967	0.770	0.949	0.950	0.774
<i>Rhipicephalus compositus</i> (301)	0.813	0.803	0.778	0.808	0.932	0.910	0.871	0.843	0.877
<i>Rhipicephalus evertsi</i> (1964)	0.879	0.846	0.868	0.891	0.919	0.802	0.866	0.864	0.756
<i>Rhipicephalus kochi</i> group (158)	0.853	0.827	0.784	0.840	0.959	0.916	0.946	0.896	0.856
<i>Rhipicephalus longus</i> (201)	0.756	0.730	0.728	0.754	0.887	0.854	0.810	0.781	0.865
<i>Rhipicephalus lunulatus</i> (191)	0.814	0.824	0.778	0.844	0.880	0.849	0.818	0.797	0.805
<i>Rhipicephalus maculatus</i> (115)	0.848	0.752	0.823	0.785	0.981	0.894	0.957	0.885	0.861
<i>Rhipicephalus pravus</i> (701)	0.860	0.840	0.817	0.865	0.931	0.860	0.859	0.840	0.790
<i>Rhipicephalus pulchellus</i> (394)	0.850	0.803	0.871	0.857	0.976	0.935	0.929	0.858	0.741
<i>Rhipicephalus punctatus</i> (128)	0.770	0.771	0.770	0.873	0.966	0.920	0.935	0.942	0.891
<i>Rhipicephalus sanguineus</i> (1124)	0.784	0.766	0.760	0.787	0.796	0.759	0.718	0.723	0.589
<i>Rhipicephalus senegalensis</i> (216)	0.812	0.799	0.802	0.836	0.911	0.873	0.867	0.877	0.846
<i>Rhipicephalus simulans</i> (1188)	0.862	0.855	0.835	0.853	0.885	0.843	0.832	0.815	0.750
<i>Rhipicephalus sulcatus</i> (109)	0.761	0.739	0.767	0.812	0.888	0.845	0.833	0.828	0.592
<i>Rhipicephalus tricuspis</i> (278)	0.794	0.741	0.787	0.796	0.879	0.854	0.828	0.827	0.802
<i>Rhipicephalus zambeziensis</i> (139)	0.720	0.840	0.812	0.855	0.982	0.953	0.962	0.963	0.886

Notes: Values of *n* refer to the number of quarter-degree squares from which ticks of that species were collected (these were given value 1 for the analysis). The rest of the column headings refer to the logistic regression predictor(s) from which the AUC values were obtained: Climate, from climatic categories; Veg, from White's (1983) vegetation map; Grid6, from 6 × 6 degree grid; Politic, from political boundaries; Clim-37, using elevation and monthly means for minimum temperature, maximum temperature, and rainfall; Mrfall, monthly rainfall; Mmint, mean monthly minimum temperature; Mmaxt, mean monthly maximum temperature; NDVI, mean monthly Normalized Difference Vegetation Index; Elev, elevation; ANDVI, mean annual NDVI; Arfall, mean annual rainfall; Amint, mean annual minimum temperature; and Amaxt, mean annual maximum temperature. Note that the values of Clim-37 for species with *n* < 150 are not strictly reliable due to the possibility of slight over-fitting of these models.

keeping all factors as constant as possible, and changing only the placing of categories in space. Before I could draw strong conclusions from this analysis, I had to put the results in context by establishing the effects of differing category numbers and category shapes on the fit of the logistic regression.

The categorical data analysis showed that climate is a better predictor of tick distributions than vegetation type. The next logical step was to separate the climatic data into different components, and compare these to one another to define more precisely what the key variables were. These data were all continuous, therefore



TABLE 2. Extended.

Elev	ANDVI	Arfall	Amint	Amast
0.829	0.805	0.821	0.701	0.784
0.874	0.651	0.600	0.557	0.708
0.788	0.669	0.574	0.745	0.774
0.772	0.623	0.605	0.543	0.585
0.770	0.662	0.587	0.763	0.796
0.619	0.755	0.756	0.565	0.595
0.595	0.797	0.758	0.711	0.760
0.828	0.790	0.717	0.535	0.678
0.834	0.702	0.649	0.556	0.686
0.664	0.803	0.762	0.577	0.604
0.694	0.736	0.740	0.513	0.646
0.713	0.738	0.708	0.515	0.611
0.659	0.738	0.706	0.507	0.629
0.632	0.513	0.515	0.542	0.506
0.674	0.676	0.731	0.709	0.598
0.754	0.713	0.677	0.657	0.731
0.743	0.688	0.758	0.805	0.694
0.771	0.754	0.718	0.578	0.744
0.809	0.684	0.655	0.498	0.630
0.795	0.779	0.734	0.673	0.772
0.709	0.741	0.709	0.635	0.742
0.621	0.831	0.846	0.508	0.675
0.692	0.728	0.672	0.588	0.666
0.901	0.716	0.651	0.639	0.803
0.514	0.682	0.656	0.523	0.534
0.538	0.603	0.554	0.626	0.630
0.731	0.599	0.567	0.659	0.688
0.666	0.610	0.581	0.627	0.639
0.810	0.795	0.726	0.747	0.822
0.701	0.722	0.571	0.849	0.905
0.812	0.632	0.467	0.960	0.945
0.707	0.697	0.656	0.631	0.745
0.805	0.558	0.506	0.965	0.924
0.833	0.760	0.702	0.679	0.804
0.731	0.660	0.563	0.857	0.891
0.774	0.808	0.777	0.633	0.757
0.822	0.679	0.623	0.727	0.785
0.824	0.810	0.731	0.732	0.827
0.676	0.827	0.831	0.522	0.620
0.706	0.736	0.760	0.615	0.670
0.800	0.725	0.653	0.562	0.666
0.825	0.670	0.629	0.562	0.697
0.820	0.558	0.450	0.530	0.650
0.847	0.759	0.698	0.703	0.817
0.595	0.665	0.661	0.518	0.598
0.627	0.749	0.797	0.742	0.581
0.763	0.708	0.654	0.606	0.701
0.596	0.726	0.717	0.541	0.572
0.746	0.763	0.722	0.615	0.719
0.777	0.656	0.439	0.670	0.661

categorization was unnecessary. With monthly and annual data now available, however, a second categorization question, in time rather than in space, arose: Was the predictive ability of monthly or annual data higher? As before, the results are based on comparisons of the ability of different variables to predict the distributions of 50 different tick species across Africa. Finally, having taken the data apart, I put the key components together in a single large logistic regression. The concurrent increase in overall predictive power supported my hypothesis that the monthly covariance of rainfall and temperature was the best correlate of tick distributions. The variables used in each of the three main sets of comparisons are summarized in Table 1.

The results of each individual logistic regression were assessed using the AUC (Area Under the Curve) of a ROC (threshold Receiver Operating Characteristic) plot. The method is described in more detail by Fielding and Bell (1997), and Cumming (2000a). AUCs are affected by sample size, and in particular by the ratio of localities from which a species has been collected to localities from which it has not. By keeping this ratio constant for different models, however, and by only comparing sets of results generated for the same species, the ratio-dependent effects become unimportant. One of the advantages of the AUC as a measure of the fit of the regression model is that it is unaffected by collinearity and spatiotemporal autocorrelation (Fig. 2), problems that make interpretation of the individual weightings of variables in complex equations virtually impossible. Each individual regression was evaluated using the AUC statistic. To establish general trends in model fit, the AUCs from different regressions were then compared using a Friedman two-way ANOVA (followed by Wilcoxon signed-ranks tests) as if they were nonparametrically distributed means. All of the meta-analyses were performed on the results given in Table 2, comparing data only for the same species and for similar variable types so that potentially confounding factors would cancel one another out.

#### *Tick data*

Individual tick distribution records were assembled from published sources (Fig. 3); the total number of records was 34 063. Full details of the sources consulted are given by Cumming (1999a). The data were collected over the period 1900–1997, and most collections occurred between 1950 and 1985. The collection records were at varying degrees of accuracy; many were entered from maps using a Calcomp Drawing-board III digitizer, and others from place names or coordinates given by the collector(s). Coordinates for collection localities were obtained from the on-line National Imagery and Mapping Agency database (NIMA 1999) where necessary. All analyses were done at a resolution of  $0.25 \times 0.25$  degrees to allow some leeway for error.

#### *Environmental data*

Climate and elevation data for Africa were taken from the Centre for Resources and Environmental Studies (CRES) database published on CD-ROM by Hutchinson et al. (1996). This consists of 60-yr mean (1920–1980) interpolated estimates on a monthly basis for minimum temperature (from 1504 stations), maximum temperature (1499 stations), rainfall (6051 stations), and elevation (based on 1:1 000 000 scale air navigation charts). The digital elevation model (DEM), and the variables that it is used to predict, cover Africa on a grid spanning 17.5 W to 51.5 E and 37.5 N to 35.0 S, at a spatial resolution of 0.05 degrees, and with a standard error for elevation ranging between 20 and 150

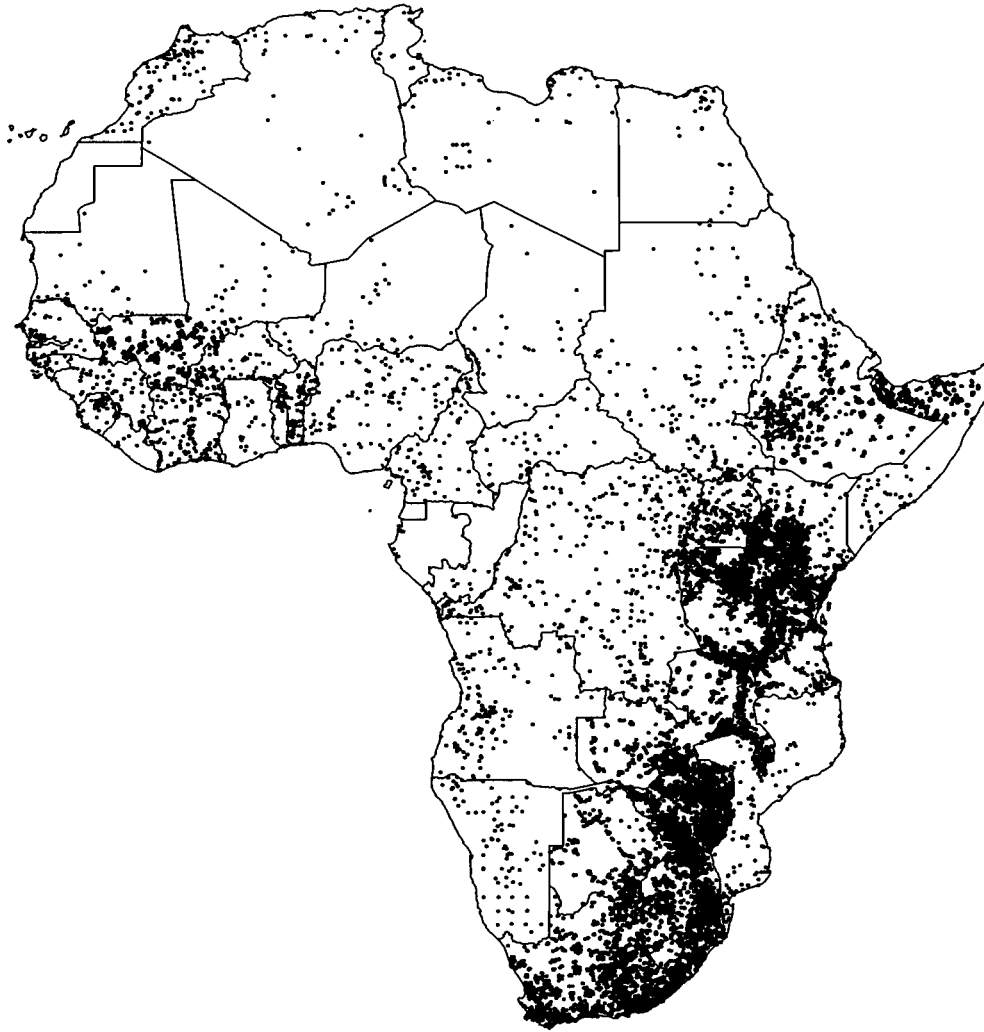


FIG. 3. Localities (indicated by dots) in Africa from which at least one tick collection records was obtained;  $n = 34\,063$  individual collections. The black lines are political boundaries. Collection localities for species that are not discussed in this paper are included in order to give an idea of the distribution of sampling effort. Full details of the origin of this data set can be found in Cumming (1999a). Reprinted from Cumming (1999a) with permission from CABI Publishing.

meters (Hutchinson et al. 1996). Madagascar was excluded from the analysis because of its different history, and unique combination of indigenous and exotic ticks.

A nine-year mean index of primary production based on satellite data, NDVI (Normalized Difference Vegetation Index), was obtained from the African Real Time Environmental Monitoring using Meteorological Satellites program (ARTEMIS) of the Food and Agriculture Organization of the United Nations (FAO); further details of the processing of this data set can be found in Rogers et al. (1996). Monthly NDVI values were obtained at four-km resolution from the Pathfinder satellite data set, kindly made available to me by the TALA (Trypanosomiasis And Land use in Africa) group at Oxford University, and used to obtain monthly mean images. These data cover the period from August

1981 to August 1984, and were manipulated using the software package Imagine (ERDAS 1998). The 12 images from 1987 were all excluded due to large numbers of missing pixels, as were May to August of 1994, and May for 1986–1989, inclusive. Monthly means were thus based on 12 yr of data for most months, with the exceptions of May (8 yr), June (10 yr), and July (11 yr).

Many of the images had isolated pixels missing. To correct the entries for these cells, I took the 12 monthly mean maps at 0.05 degree resolution, and rewrote all non-water pixels that were below the acceptable value for NDVI to a median value. I then gave the mean value of its 24 nearest neighbors to each pixel in each image that had the median value. This procedure would have resulted in either a slight accentuation, or a slight homogenization of local differences, depending on the

surrounding pixels, but the averaging of blocks of pixels in the next step would have rendered these errors negligible. Finally, the resolution of each image was decreased to  $0.25 \times 0.25$  degrees by taking the mean value within each  $0.25 \times 0.25$  degree cell. The exercise of replacing missing pixels with median values prior to averaging within cells meant that, at most, the error associated with a single missed pixel would be 0.04; and having adjusted the medians to reflect the values around the cell, the mean error would be even lower. Given the large sample sizes used in the analysis and the small numbers of missing pixels, these errors should be insignificant for analysis as a whole.

Vegetation types were taken from a digital version of White's (1983) vegetation map of Africa that includes 82 vegetation categories (Fig. 4a). The grids used in part of the analysis were generated in the software package MapInfo™ (MapInfo 1998).

The resolution (pixel size) of continuous data sets was decreased from  $0.05 \times 0.05$  degrees to  $0.25 \times 0.25$  degrees by taking the mean value (for each variable) of all points within each  $0.25 \times 0.25$  degree cell. Points for which climatic data were not available, such as those in lakes, were excluded from the analysis. Categorical values were extracted from the relevant map for each of the corresponding cells.

The tick data consisted of a single georeferenced column (40 020 rows, one for each  $0.25 \times 0.25$  degree cell) of binary values for each species, registered 1 for positive records, and 0 for absences or uncollected cells. This was used to develop logistic regressions from the set of predictor variables. The initial set of predictors consisted of 40 020 georeferenced rows covering Africa at 1/16 degree resolution for mean monthly rainfall (12 columns), mean monthly maximum temperature (12 columns), mean monthly minimum temperature (12 columns), mean monthly NDVI values (12 columns), elevation, vegetation type (82 categories), a  $6 \times 6$  degree grid (96 categories), political identity (84 categories), and nine-year annual mean NDVI values (a single column). Continuous variables were standardized prior to analysis by subtracting the mean and dividing by the standard deviation, a procedure which has no effect on the regression output, but makes the formation of climatic clusters less likely to be biased by the differing magnitudes of individual variables.

#### *Statistical details*

I compared the potential of different variables to limit the ranges of African tick species using a series of logistic regressions. The accuracy of each regression was assessed using the Area Under the Curve (AUC) of an ROC (threshold Receiver Operating Characteristic) plot, estimated in the software package STATA (Stata 1998). If all  $0.25 \times 0.25$  degree cells in which the occurrence of study species has been registered are termed positives, and all cells where the species have not been recorded are termed negatives, then "sensi-

tivity" is defined as the probability that the model produces a positive result in a positive locality, and "specificity" is the probability that the model produces a negative result in a negative locality (Table 3; Agresti 1996). Plotting all sensitivity values on the y-axis against their equivalent ( $1 - \text{specificity}$ ) values produces an ROC plot (Fielding and Bell 1997). The AUC of the ROC plot offers a means of comparing the logistic regression results in an empirical manner, without the need to rely on a particular probability cut-off level to assign significance; the value of the AUC generally ranges between 0.5 and 1, with 0.5 indicating a random fit, and 1 a perfect fit. A value of 0.8 for the AUC means that in 8 out of 10 instances, random selection of a point from the group of known occurrences will be associated with a probability that is greater than a random selection from the negative group (Fielding and Bell 1997). A worked example of manual AUC calculation is given by Cumming (2000a).

One of the virtues of using AUC values to quantify the regression's fit is that they offer an assessment based entirely on predicted probability values. Correcting for collinearity affects the weightings of different variables within the equation, but has no effect on the predicted probability value that is ultimately associated with a given cell (Fig. 2). Since no attempt is made to interpret coefficients in this paper, correcting for collinearity in this instance is irrelevant. Similarly, the main effects of autocorrelation are on coefficient values rather than on the probabilities associated with individual cells (Cumming 2000a). A further advantage of using between-model comparisons over alternative methods is that any nonrandom biases introduced into the probability values (such as through averaging within grid cells, for example) are canceled out. The same species occurrence data are used for each comparison, and variables that are compared to one another are identical in nearly every respect but the fine details of their values. The categorical variables differ mainly in the spatial position of the boundaries, and the continuous variables, with the exception of NDVI, are all interpolated from the same digital elevation model. Consequently, neither collinearity nor spatial autocorrelation affect the conclusions of the analysis.

The comparison of climate and vegetation as determinants of tick distributions is complicated by the differing qualities of the available coverage for Africa. The vegetation data is an externally imposed definition of natural classes over what is essentially a continuous variable. Since the resolution of these data could not be improved, the climatic data had to be similarly categorized before vegetation type and climate could be compared. Climatic categories were created using the K-means clustering procedure in the software package SPSS (1999), where the desired number of clusters (= categories) is specified by the user. The standardized data used to produce these natural climatic categories included monthly mean minimum and mean maximum

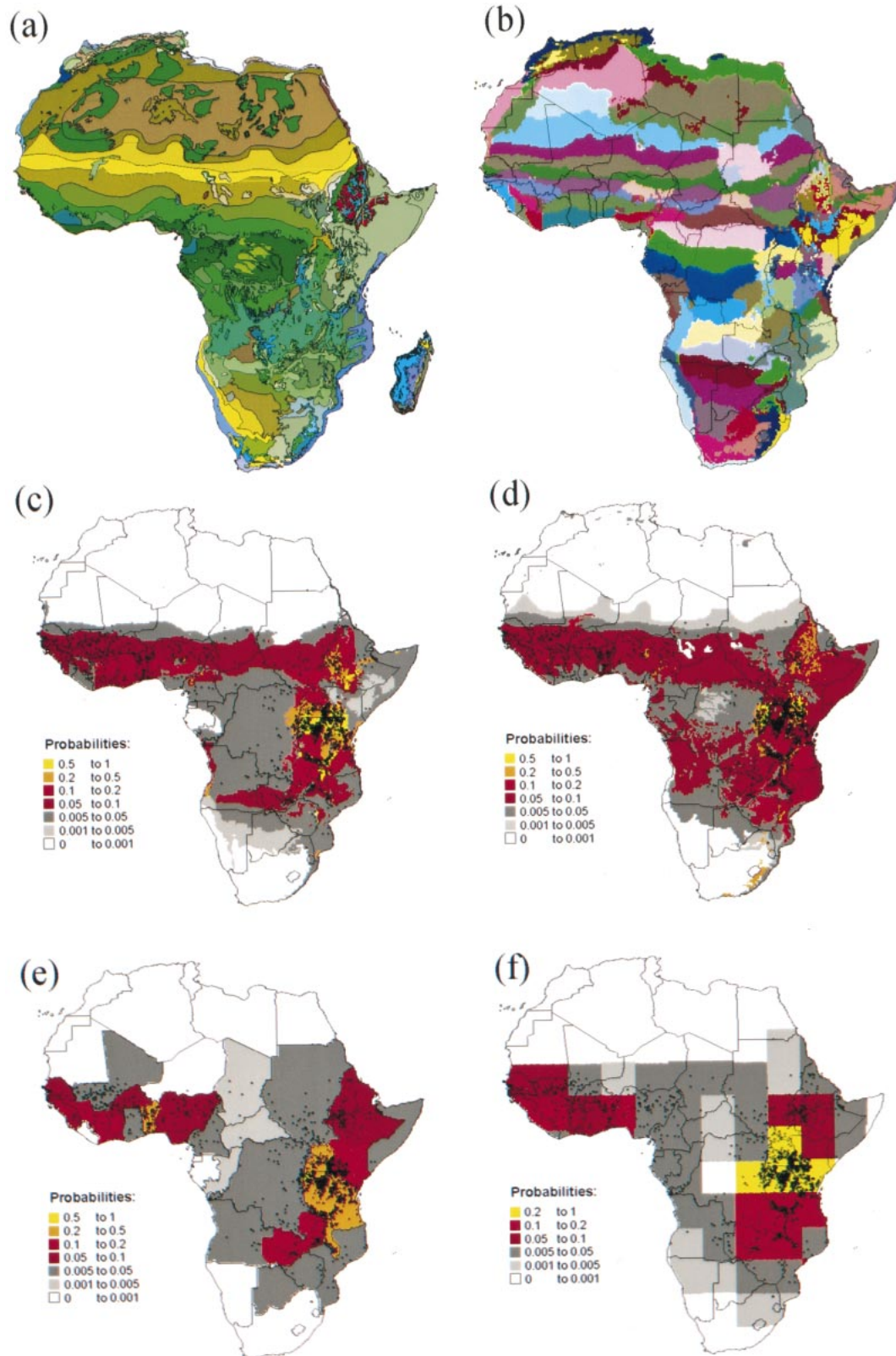


FIG. 4. **Vegetation, climate, and an example of logistic regression model maps of Africa.** (a) re-drawn map of Africa based on White (1983). Distinct polygons indicate different vegetation classes. In a few cases, different classes are shaded with the same color. (b) Map of 82 natural climatic categories derived from clustering rainfall, temperature, and elevation data. Note that no spatial information was included in the clustering procedure. (c–f) **Examples of logistic regression models**



temperature, monthly mean rainfall, and elevation (a total of 37 variables). I term the categories “natural” because they reflect real differences between areas, rather than the more “artificial” categories imposed by a coordinate-based grid.

In logistic regression models, categorical data are coded as one fewer binary (1–0) dummy variables than there are categories. To investigate the effect of the number of categories on the AUC estimate of regression accuracy, I first produced a series of logistic regression models using different numbers of climatic categories as predictors. To make sure that the irregular shapes of these categories were not unduly influencing the test of the effect of category number on accuracy, I also produced a series of logistic regression models based on uniformly shaped climatic grids with cell dimensions of  $6 \times 6$ ,  $8 \times 8$ ,  $10 \times 10$ ,  $15 \times 15$ ,  $20 \times 20$ ,  $30 \times 30$  and  $40 \times 40$  degrees, respectively. Each instance was replicated for a subset of 26 of the 50 tick species studied, and the means and standard deviations of the AUC values calculated.

Based on locality data for all 50 tick species, I then used the AUC statistic to compare the predictive ability of individual logistic regression models based on vegetation type (82 categories), climate (82 categories), the  $6 \times 6$  degree climatic grid (96 categories), and the countries of Africa (84 categories), respectively. This stage yielded four logistic regression models for each of the 50 species in the analysis (Tables 1 and 2). The regressions based on political categories test for localized collecting activity, while those from the grid provide an artificial categorization that in theory should provide a less adequate model than the more natural boundaries of vegetation and climate categories. The four 50-row columns of AUC data produced from these analyses (Table 2) were compared as a group using a single Friedman two-way analysis of variance, followed by a series of Wilcoxon signed-ranks tests to establish which variable most affected the Friedman statistic (Siegel and Castellan 1988). The relatively large number of categories in the data sets may suggest that some of the logistic regressions based on smaller sample sizes of collection records were over-fitted. In fact this is not the case, because only categories that contain some records were used by the analysis. For example, the vegetation regression for *Margaropus winthemi* ( $n = 95$ ) had nonzero coefficients for only 15 of the potential 82 categories.

Because of problems with collinearity and autocorrelation, the values of the coefficients for individual variables within the logistic regression equations cannot be used to make reliable statements about biological

TABLE 3. Definitions of the terms “sensitivity” and “specificity.”

Predicted	Observed	
	+	–
+	<i>a</i>	<i>b</i>
–	<i>c</i>	<i>d</i>

Notes: Plus (+) symbols represent presence, and minus (–) symbols represent absence. Sensitivity is defined as  $a/(a + c)$ , and specificity as  $d/(b + d)$ . ROC plots use  $1 - \text{specificity} = b/(b + d)$ ; total cases,  $n = a + b + c + d$ .

meaning (Cumming 1999b, 2000b). To directly compare the predictive abilities of a large set of inter-related variables (such as rainfall, temperature, and vegetation type), it is then necessary to compare the predictions of entire regression equations rather than taking the alternative approach of drawing inferences from a single equation that incorporates all the variables. To establish the predictive abilities of different continuous variables, I initially ran four logistic regressions for each of the 50 species under consideration, each model using 12 monthly values for one of rainfall, minimum temperature, maximum temperature, and NDVI. No categorical data were used in this analysis. To include elevation data in the comparisons, and to investigate the effects of temporal scale, I then performed a separate analysis in which the three 12-variable monthly climatic data sets were converted into three single-variable annual means. The logistic regression results from these data were compared to those from elevation and the nine-year mean NDVI data, again using AUC values to assess the predictive ability of each regression. No model-specific adjustment to the AUC is necessary for these analyses because it is based on a ratio rather than a single critical threshold value. The AUCs derived from these logistic regressions were again compared using a Friedman two-way analysis of variance and Wilcoxon signed-ranks tests (Siegel and Castellan 1988). Details of the models used in each of the three main sets of comparisons are summarized in Table 1.

## RESULTS

### *Effects of clustering on model accuracy*

Results from regressions using different numbers of natural climatic categories showed that when the area under consideration is held constant, splitting it into more categories causes accuracy to increase rapidly at first and then to level off (Fig. 5). Above a certain point ( $\sim 20$  clusters in this instance), the addition of further categories made little difference to the AUC estimate of model accuracy. This result held true when the

←

for *Amblyomma variegatum*. The maps show how the distribution of *A. variegatum* (black dots indicate positive collection localities) can be estimated using (c) natural climatic clusters, (d) vegetation categories, (e) political boundaries, and (f) a  $6 \times 6$  degree grid.

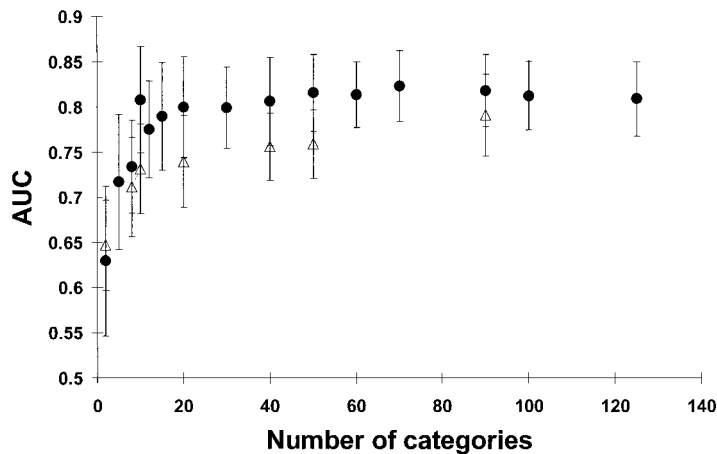


FIG. 5. The effect of the degree of splitting into categories on the AUC estimate of model accuracy. This plot shows how model accuracy changes with the number of categories for models using different numbers of natural climatic categories (solid circles) and different numbers of regularly shaped cells (open triangles). The area over which the model is developed remains constant in each case. The bars show one standard deviation above and below each point (the data were derived from logistic regression models for 26 tick species).

shapes of cells were held constant and the number of categories was increased (Fig. 5). The AUCs from climatic clusters were routinely higher than those from the climatic grids, particularly at higher numbers of categories. Because of limitations imposed by the sample sizes of the tick data, the predictive ability of models using >125 categories was not tested. The fact that using 40 020 continuous data points provides a much more accurate result than the categorical data suggests that adding further categories would probably result in a very gradual increase in predictive ability. In the range of 50–100 categories, the precise number used in predicting tick distributions is largely irrelevant to the model's overall accuracy.

#### Comparison of categorical variables

The regions defined by each of the categories for vegetation type, climate, political categories, and the  $6 \times 6$  degree grid are shown in Fig. 4a,b, and Fig. 6. The mean values of the AUCs for logistic regression models of 50 different tick species (Table 2 and Fig. 4c–f) suggest that political boundaries were the best predictor (mean AUC = 0.818), followed by climate (mean AUC = 0.817), vegetation type (mean AUC = 0.799), and the  $6 \times 6$  grid (mean AUC = 0.795). There was a significant difference between these AUCs when considered for all 50 species (Friedman two-way ANOVA test statistic 27.582,  $P < 0.001$ ,  $n = 50$ ). Comparing the rank sums from the analysis (Table 4), the variables fall into two classes: Climate and political boundaries have similar predictive abilities, while the  $6 \times 6$  grid and vegetation type are similar.

TABLE 4. Rank sums for different categorical variables from the Friedman two-way analysis of variance.

Variable	Rank sum
$6 \times 6$ degree grid	93.5
Vegetation type	110
Political boundaries	148
Climate (82 categories)	148.5

Comparison of variables at an individual level using Wilcoxon signed-ranks tests (Siegel and Castellan 1988) supports the results of the Friedman two-way ANOVA. At an individual level, the predictive abilities of both climate and political boundaries differ significantly ( $P < 0.05$ ) from each of vegetation type and the  $6 \times 6$  degree grid, but not from one another, while vegetation type does not differ from the  $6 \times 6$  grid (Table 5).

#### Comparison of continuous variables

**Mean monthly variables.**—The predictive abilities of the mean monthly values for rainfall, minimum temperature, maximum temperature, and NDVI (12 variables in each case, at  $0.25 \times 0.25$  degree resolution) differed significantly (Friedman two-way ANOVA test statistic 60.72,  $P < 0.001$ ,  $n = 50$ ). Mean monthly NDVI, a surrogate for plant photosynthetic activity, is the worst predictor, and minimum temperature is the best (Table 6). When NDVI was removed from the analysis, the predictive abilities of the other three variables did not differ significantly (Friedman two-way ANOVA test statistic 2.08,  $P \leq 0.353$ ,  $n = 50$ ).

The logistic regression models based on 12 monthly mean values for a single variable are all weaker than the one using all 37 rainfall, temperature, and elevation variables (Friedman two-way ANOVA; test statistic 144.85,  $P \leq 0.001$ ,  $n = 50$ ; Table 7).

**Mean annual variables.**—The predictive abilities of mean annual rainfall and rainfall totals, mean annual NDVI values, and elevation also differed significantly (Friedman two-way ANOVA test statistic 65.71,  $P \leq 0.001$ ,  $n = 50$ ; Table 8). Individual Wilcoxon signed-ranks tests supported this result in each case ( $P < 0.05$ ), except for the pairs rainfall–maximum temperature and rainfall–minimum temperature (Table 9). Annual mean NDVI is a better predictor of tick distributions than the annual means for minimum temperature, maximum temperature, or rainfall.

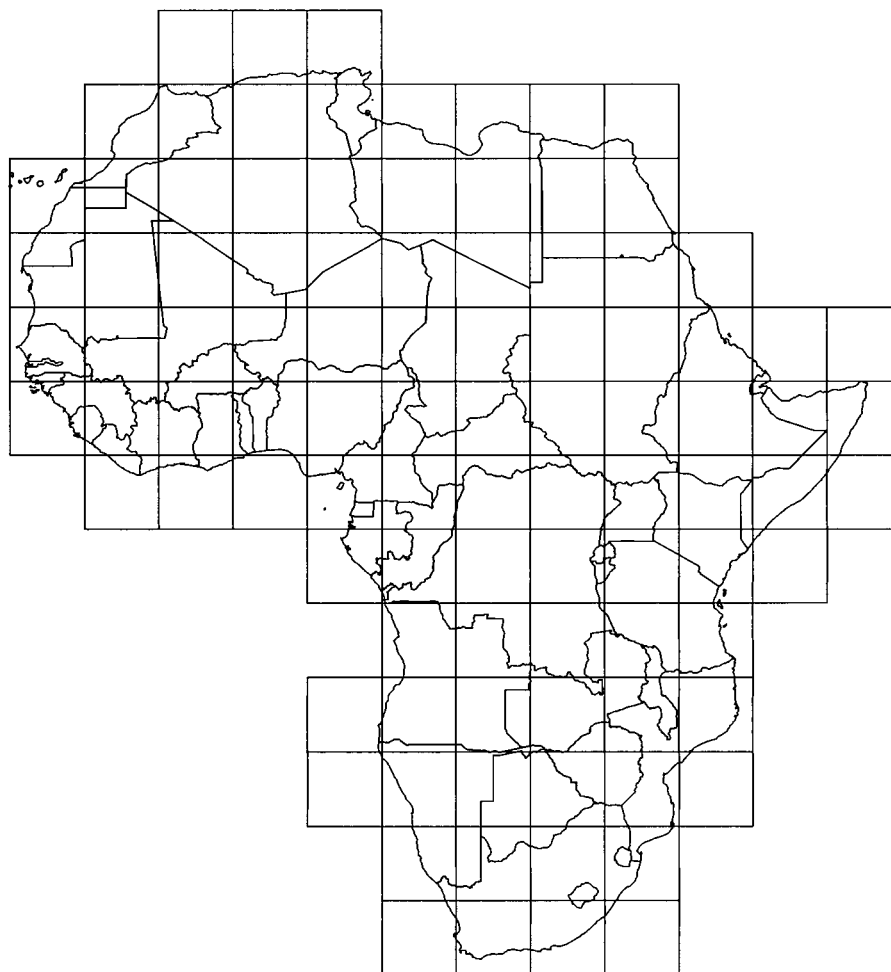


FIG. 6. Map showing political boundaries and the  $6 \times 6$  degree grid used as a control in comparisons of categorical variables.

## DISCUSSION

### *Categorical variables*

The categorical analysis shows that climate is a significantly better predictor of tick distributions than vegetation type; categories produced using rainfall and temperature data describe tick species ranges better than do vegetation categories. This result is supported by the low predictive ability of the  $6 \times 6$  degree climatic grid. The high predictive ability of political categories highlights the patchiness of the tick data; while some countries have been well surveyed, very little is

known about tick distributions in others (Fig. 3). The comparison of political and climatic regions is further complicated by the tendency of international boundaries to follow natural landmarks such as rivers and watersheds. This result serves to confirm that the methods will detect the differences between categories that genuinely describe the distribution of collection records and those that do not.

The predictive ability of vegetation type does not differ significantly from that of a  $6 \times 6$  degree grid of regularly shaped cells. A truly random null model would use points that were not located in spatially dis-

TABLE 5. Results of Wilcoxon signed-ranks tests comparing variables individually.

Variable	Climate	Vegetation type	$6 \times 6$ grid
Vegetation type	-3.34***		
$6 \times 6$ degree grid	-3.53***	-1.16	
Political	-2.41	3.07*	3.61***

Notes: The numbers are Wilcoxon's  $Z$  ( $n = 50$ ).

\*  $P < 0.05$ ; \*\*\*  $P \leq 0.001$  (two-tailed  $P$  values).

TABLE 6. Rank sums from a Friedman two-way ANOVA comparing models for 50 tick species based on mean monthly values for continuous variables.

Variable	Rank sum
Mean monthly NDVI	61
Mean monthly rainfall	140
Mean monthly maximum temperature	143
Mean monthly minimum temperature	156

TABLE 7. Rank sums comparison of 12-variable models to a single model using the variables mean monthly minimum temperature, mean monthly maximum temperature, mean monthly rainfall, and elevation.

Variable	Rank sum
NDVI	61
Rainfall	140
Maximum temperature	143
Minimum temperature	156
37 variables	250

crete units. The nonrandom predictive ability of vegetation type, with all the AUCs well over 0.5 (Table 2), is a direct consequence of the spatial integrity of the vegetation classes. The similar AUCs from vegetation type and the  $6 \times 6$  grid indicate that tick species ranges generally do not follow particular vegetation classes any more than one would expect by chance; vegetation types do not constitute natural boundaries for tick species ranges.

It would be interesting to extend these comparisons to cover vegetation structure as well as vegetation type. Unfortunately, pan-African data for vegetation structure are not currently available. Tick survival is affected by microclimate (e.g., Londt and Whitehead 1972, Needham and Teal 1991), and ticks may be more influenced by whether or not the trees offer some protection from direct sunlight than the species of tree in the woodland. Although vegetation type will be a surrogate for certain kinds of structural difference (e.g., between grassland and forest), it also separates some structurally similar areas and lumps together some structurally different ones.

#### Continuous variables

Of the continuous variables that were compared on a monthly basis, minimum temperature is a slightly better predictor of tick distributions than either rainfall or maximum temperature, and all of these variables do better than NDVI. At an annual mean level, however, NDVI is a better predictor of tick distributions than are climatic factors. This difference between monthly and annual results is intriguing, and probably relates to differences in the speed at which fluctuations occur in the variables considered. Plant productivity changes in response to climatic changes, but it does so more slowly than the changes themselves and is lagged behind them

TABLE 8. Rank sums comparison of mean annual values and elevation from a Friedman two-way analysis of variance on annual mean variables and elevation.

Variable	Rank sum
Minimum temperature	88
Rainfall	129
Maximum temperature	148
Elevation	180
NDVI	205

TABLE 9. Results of Wilcoxon signed-ranks tests comparing mean annual variables individually.

	Elevation	NDVI	Rainfall	Min temp
NDVI	2.76*			
Rainfall	-2.99*	-5.17***		
Min temp	-4.16***	-5.53***	-1.95	
Max temp	-2.86*	-4.33***	1.36	4.73***

Notes: The numbers are Wilcoxon's Z statistic. Min temp, mean annual minimum temperature; max temp, mean annual maximum temperature; Rainfall, mean annual rainfall; NDVI, mean annual Normalized Difference Vegetation Index (a measure of plant productivity).

\*  $P < 0.05$ ; \*\*\*  $P < 0.001$ .

(Eklundh 1996), making NDVI a less sensitive variable than temperature or rainfall at smaller temporal scales. At larger temporal scales, seasonal differences in temperature and rainfall are smoothed; the less intense, but more constant level of plant productivity then becomes the more reliable predictor.

The high predictive ability of elevation is not surprising given its close correlation to temperature and rainfall (Eklundh 1996). Although elevation may be the best single predictor variable for use in estimating tick distributions, its lack of temporal variation makes it a less sensitive predictor than variables that vary temporally as well as spatially. The monthly mean values for minimum temperature, maximum temperature, and rainfall have similar predictive abilities to one another. This may be due to their correlation with one another, but the much greater accuracy of regressions that used all three of the climatic variables suggests that tick survival and reproduction are dependent on the covariance between temperature and rainfall, rather than on one of these variables alone. Such a hypothesis is consistent with smaller scale studies: water balance is of key importance in tick survival (Needham and Teal 1991), and both temperature and moisture availability have significant effects on tick developmental rates (Dipeolu 1989), and hence on the population growth rate. For example, for *Amblyomma hebraeum* in South Africa Norval (1977) found that there were declines in population density following hot dry periods, and secondary peaks following rain. Warm, dry conditions thus tend to result in increased tick mortality while warm, wet conditions result in increased population growth.

#### General implications

Taken in the context of current knowledge, the results imply that the distributions of African ticks are typically determined by the direct effects of climate. Biotic variables that respond to the same abiotic conditions, such as vegetation type and host distributions, may be important in creating heterogeneity in tick distributions at smaller scales (e.g., Minshull and Norval 1982), but play a subordinate role in limiting the species ranges of ticks at broad spatial scales. This conclusion is supported by the smaller scale findings of



several previous studies (e.g., Walker 1974, Dipeolu 1989, Needham and Teal 1991, Randolph 1994), but differs from others (e.g., Lessard et al. 1990, Norval et al. 1994) in its focus on climate rather than on environmental structure or host-related factors. That climate should ultimately set limits on tick species ranges makes good sense in light of their small body size, their relative immobility, and the high proportion of their lifecycle that is spent off-host (Needham and Teal 1991).

Given the large species ranges and apparently high dispersal ability of many ticks, the long-term eradication of cattle ticks using pesticides will be difficult to achieve unless carried out at very large spatial scales. Unless control methods are applied throughout a given climatic region, ticks are likely to recolonize areas from which they have been "eradicated" (e.g., Lawrence et al. 1980). The dependence of ticks on climate does have some practical advantages in that it simplifies attempts at modeling the incidence of tick-borne disease (e.g., Duchateau et al. 1997). Seasonal and/or annual changes in the distributions of both ticks and tick-borne diseases could be relatively simple to predict if reasonable projections of climatic conditions can be obtained.

If tick species ranges are determined by climate, then their biogeography should reflect the history of climatic changes in the regions where they occur. It seems likely that new tick species could have formed as a consequence of climate-driven expansion and contraction of their ranges, rather than through tick-host cospeciation (Cumming 2000b). The suggestion made by Klompen et al. (1996) that "biogeography and ecological specificity should be accorded a far more prominent role in tick evolution" is strongly supported by the results of this study.

These results should be further tested using controlled studies at smaller scales. The main hypotheses that emerge for the long-term survival of tick populations and the distributions of ticks at smaller scales are (1) individual survival in a given area is more closely correlated with climatic conditions than with vegetation type; (2) vegetation structure is more important for individual survival than vegetation type; and (3) increased mortality rates under natural conditions are more likely to result from coincident, unfavorable variations in both rainfall and temperature than from the equivalent variation in only one of these variables. Comparative laboratory studies of the immediate effects of temperature, desiccation, and microhabitat availability on ticks of different species should be useful in relating small- and large-scale processes; if the extent of the species range is dependent on individual habitat tolerances, then (4) ticks with larger ranges should be more resistant to small-scale climatic changes.

Lastly, the use of between-model comparisons offers a valuable alternative to within-model comparisons of variables when establishing the potential of different

environmental factors to limit the distribution of a given species; careful experimental design can allow the comparison of multiple, intercorrelated variables in a statistically sound manner.

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