

A COMPUTERISED SYSTEM FOR MATCHING CLIMATES IN ECOLOGY

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ABSTRACT

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A computer-based system (CLIMEX) is described which enables the prediction of an animal's potential relative abundance and distribution around the world, using biological data and observations on geographical distribution. Separate indices describe the potential of a population firstly to grow, and secondly to persist through climatically unfavourable periods. The indices are then combined to give an "Ecoclimatic Index", which describes the overall climatic favourability of any location for that animal.

The system is applicable in such areas as quarantine, biological control, pest management and epidemiology. Examples from veterinary entomology, using the ticks *Boophilus microplus*, *Rhipicephalus appendiculatus* and *Amblyomma variegatum*, and the flies *Haematobia* spp., are used to illustrate how CLIMEX can provide insight into likely changes in population size within years, between years and between places. The caveats usually associated with climatic matching are reiterated.

INTRODUCTION

Climate determines the distribution and abundance of most poikilothermic animals (Andrewartha and Birch, 1954). In a given climate, physical and biological factors such as habitat and food selection and other species of animals determine the presence or absence of an animal and modify its potential population size. Human activities are also important.

In epidemiology, pest management, quarantine and biological control of weeds and insect pests, comparisons are often needed of the climatic potential of different locations to support populations of plants and animals. Climatic matching, using tables (e.g. Anon., 1975) or graphs (e.g. Walter et al., 1975), is tedious and does not take into account the response of a particular species to climate. Cook (1925) overcame some of these deficiencies by producing climatographs, and these have been widely used. He superimposed the response of an insect population to climate onto static seasonal or locational graphs of temperature and relative humidity. Messenger (1974) reviewed the

literature on bioclimatology, but reported little progress in the development of new techniques.

Meanwhile, plant ecologists were quantifying and integrating the effects of climate on plant growth. "Growth indices" were developed to compare the potential of different places and seasons for plant growth (e.g. Fitzpatrick and Nix, 1970). Gutierrez et al. (1974) used the concept to classify the favourability of different years and locations in south-eastern Australia for clover and for cowpea aphids.

We describe a computerised system, CLIMEX, for comparing the relative potential for growth and persistence of populations of poikilothermic organisms at different times and places. A principal aim of the system is to provide a single number to describe the favourability of each location for a specified animal. Such an index is useful to policy makers in particular, and can be dissected into its component parts for more detailed requirements.

The system was designed to cater for those situations where too little biological information exists on the animal to enable a useful population model to be built. As such, it can indicate only the gross features of the animal's likely distribution and abundance. It can also point to the factors that limit the distribution of an animal and to those that cause seasonal population changes. The system provides for different levels of sophistication, determined by the quality and quantity of the available data. When no biological data are available, meteorological data per se from a given place can be compared with those from elsewhere. A user's guide to CLIMEX (Maywald and Sutherst, 1985) and copies of the FORTRAN program and data base are available on request.

DERIVATION OF THE "ECOCLIMATIC INDEX"

In most parts of the world, animal populations annually experience a season which is favourable to population growth and one which is unfavourable and may even threaten their persistence. The annual size of a population will reflect the combined effects of favourable and stressful seasons. For poikilothermic animals, the two major components of climate are temperature, which gives a measure of available energy, and moisture, which is necessary for the animals to exploit that energy supply. In addition, daylength may affect the species either directly or indirectly. Given meteorological data and some estimate of the response of a population to temperature, moisture and daylength, an annual "ecoclimatic index" (*EI*) can be derived to describe the climatic favourability of a given location for that species.

The ecoclimatic index, scaled between 0 and 100, is derived as described below. An annual mean of the weekly values of a population growth index (*GI*) is determined to assess the potential for the population to increase. This is reduced by 4 stress indices to give the *EI*,

that is,

$$EI = 100 \left(\sum_{i=1}^{52} GI \right) / 52 \times [(1-CS) \times (1-DS) \times (1-HS) \times (1-WS)]$$

where the weekly population growth index $GI = TI \times MI \times LI$. TI , MI and LI are weekly temperature, moisture and daylength indices which are all scaled between 0 and 1. CS , DS , HS and WS are yearly stress indices, also scaled between 0 and 1, which describe the effects of both the duration and severity of extremely cold, dry, hot and wet conditions, respectively (Fig. 1). Details of the formulation of each index are given below, and procedures for estimation of their parameter values are described by Maywald and Sutherst (1985).

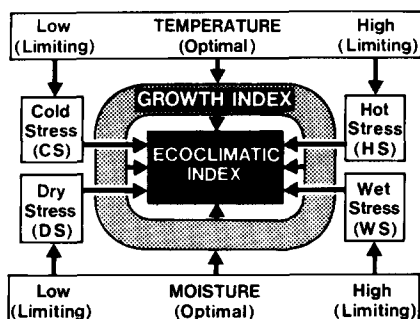


Fig. 1. Derivation of the "Ecoclimatic Index" (EI) as the product of the "Growth Index" (GI) and four stress indices.

Growth Index (GI)

Temperature Index (TI)

The temperature index describes the response of the animal population to the daily temperature cycle, approximated by a sine curve fitted to maximum and minimum temperatures. The index consists of two components, one of which (I_Q) describes the effect of temperature on development rates, while the other (I_H) describes the reduced survival rates of the animal at high temperatures. It is assumed that no population growth occurs ($I_Q = 0$) below a threshold temperature, $DV0$, and that there is an optimal temperature for population growth ($I_Q = 1$) at temperature $DV1$. Accumulated daily growth is equal to Q , the shaded area under the daily temperature curve above $DV0$, in units of day-degrees (Fig. 2). In order to scale $I_Q \leq 1$, $I_Q = Q/A$, where A is the day-degrees accumulated at the optimal temperature $DV1$ and $I_Q = 1$ when Q exceeds A . Whilst the maximum temperature is less than $DV2$, $I_H = 1$. When maximum temperatures exceed $DV2$, population growth is reduced by a high temperature effect until no growth occurs ($TI = 0$) when the temperature exceeds $DV3$. The temperature index is the product of these two components, i.e. $TI = I_Q \times I_H$. The number of day-degrees available for development is calculated and an option is available to estimate the number of generations per annum, given the number of day-degrees to complete one generation.

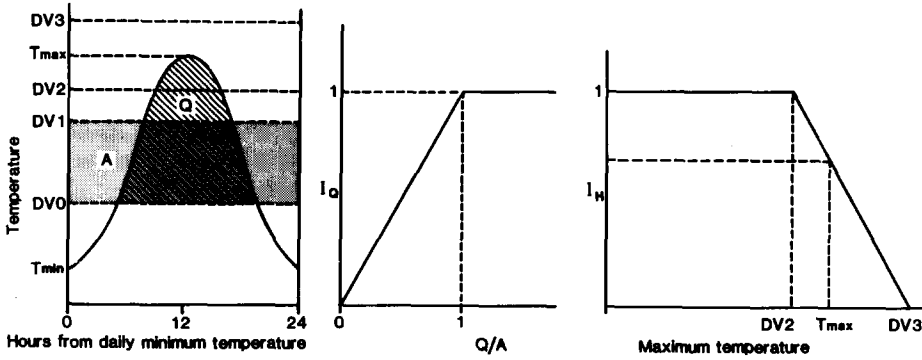


Fig. 2. The "Temperature Index" (TI) as a function of mean maximum and minimum daily temperatures (see text). Q = Area under the daily temperature cycle and above $DV0$, while A = area between $DV0$ and $DV1$ (in units of day-degrees). $TI = I_Q \times I_H$.

Moisture Index (MI)

The moisture index is derived using a soil-moisture model, which assumes that the moisture content of soil is the dominant factor determining micro-climatic conditions and the condition of vegetation. However, an option is available to use only atmospheric RH. The soil moisture balance is calculated weekly from the stored soil moisture and the current week's rainfall and evapotranspiration, as described by Fitzpatrick and Nix (1969). Maximum soil moisture storage capacity is set usually at 100 mm and the evapotranspiration coefficient is set at 0.8. Four parameters describe the population's response (MI) to soil moisture (Fig. 3). $MI = 0$ when the soil moisture is below a critical threshold ($SM0$) and when it is above a level ($SM3$) at which excessive moisture is lethal; $MI = 1$ between two intermediate soil moisture levels, $SM1$ and $SM2$, with linear interpolation between the four levels.

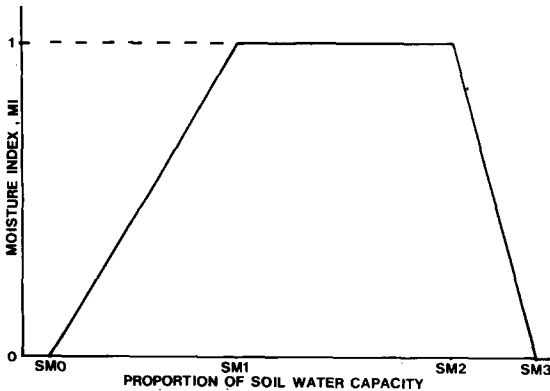


Fig. 3. The "Moisture Index" (MI) as a function of computed soil moisture availability.

Light Index (LI)

The light index is included to allow for those species whose potential to propagate or survive is affected by daylength. The effect may be direct through diapause or indirect through plant phenology, affecting animal nutrition, for example. A single parameter, DL , is used to determine whether or not the animal responds to daylength and also the nature and extent of that response. If daylength has no direct or indirect effect, LI is given a constant value of 1.0 (and so has no effect) by setting $DL = 0$. In cases where decreasing daylength reduces population growth, e.g. by affecting plant phenology, DL is made positive. LI is then less than 1.0 while daylength is decreasing, reaching a minimum value when the rate of change of daylength is at its maximum (i.e. at the autumn equinox), and returning to 1.0 after the shortest day. If population growth is inhibited by increasing daylengths, DL is given a negative value. LI is reduced to zero at a latitude of 30° for $DL = 1$.

Stress Indices

We have defined four stressful climatic conditions and describe their cumulative effects using "stress indices". Each week that the population experiences adverse conditions, we accumulate an "effective stress value", V . $V = g(S) \cdot t$ where $g(S)$ is a stress function, dependent on the magnitude of the stressful condition, S (e.g. extreme temperature) encountered, and t is the time (in weeks) that this stressful condition has persisted. The yearly stress index is the sum of these weekly values, scaled between zero and one, i.e.

$$\text{Stress Index} = \frac{\sum_{i=1}^{52} V_i}{52}$$

Each stress function, $g(S)$, has two parameters. A threshold parameter (prefix T , e.g. THS) which determines the level at which stress is accumulated, and a rate parameter (prefix H , e.g. HHS) which determines the rate of accumulation of stress (Fig. 4a). Even though $g(S)$ is a linear function of stress, S , the stress index is accumulated non-linearly with respect to time (Fig. 4b). For example, using the stress function of Fig. 4a, assume that the maximum temperature exceeds THS by an amount that results in $g(S) = 0.1$. Then, the accumulated stress, $\sum_{i=1}^t g(S) \cdot t$ will give 0.1 for Week 1, $0.1 + 0.2 = 0.3$ for Week 2, $0.1 + 0.2 + 0.3 = 0.6$ for Week 3, etc., giving the non-linear response depicted in Fig. 4b.

The parameter values of the stress functions can be changed to suit the response of each species. HS , WS and DS are usually directly relatable to maximum temperature or soil moisture, but CS can have two interpretations. Animals may die because the diurnal temperature is too low to maintain metabolism. Alternatively, they may die if exposed to excessively low temperatures, even though the mean diurnal temperature is high enough to permit development. CLIMEX provides a choice between these alternatives,

referred to as “day-degree” ($MCS = 0$) or “lethal temperature” ($MCS = 1$) options. Over-wintering mechanisms, such as diapause, can effectively reduce cold stress to nearly zero. In some cases there will be inadequate heat summation over the whole year to allow univoltine animals to complete their life cycle. In such cases, some minimum GI values will describe the cut off point.

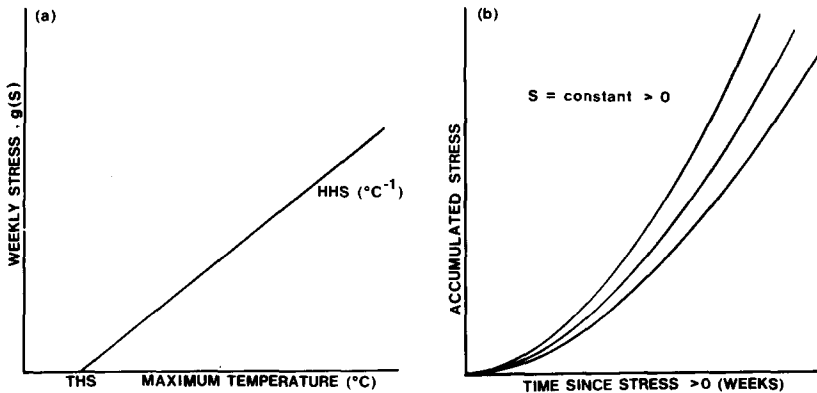


Fig. 4. The form of the stress indices. (a) Weekly stress function $g(S)$; (b) accumulated stress.

The roles of laboratory data and field observations

Parameter values for each of the indices can be estimated from different starting points, depending upon the availability of experimental data or information on the relative abundance and geographical distribution of the animal.

Laboratory measurements of the temperature and moisture requirements of animals indicate the optimal range of conditions and the extremes of temperature or moisture at which the animal is susceptible. The data cannot be used directly to derive parameter values in the field owing to differences between micro- and meso-climates. CLIMEX parameter values must reflect the response of the animal to environmental conditions, so that laboratory data provide only a starting point from which to estimate parameter values by iteration.

A second starting point is from field observations of geographical distribution and seasonal abundance. The validity of predictions from field observations alone may be limited by the restricted range of climates in the observation area or by substantial non-climatic factors in the area where parameter values for CLIMEX are chosen. For example, within the observation area, every stressing condition may not reach a maximum. This limitation may be minimised by careful choice of observation areas used to estimate parameter values. Situations where non-climatic factors have a dominant influence may be detectable by failure to obtain a satisfactory fit to the observed distribu-

tion and abundance, or by major discrepancies between parameter values derived using laboratory data on the one hand and field observations on the other. These discrepancies can be useful and informative by pointing to the existence of non-climatic or micro-climatic factors affecting the population.

Examples illustrating the use of CLIMEX

Five examples of the use of CLIMEX are given below to illustrate different aspects of its use.

(a) Cattle tick, Boophilus microplus

Boophilus microplus is widespread in the humid tropics around the world. An extensive literature exists on its temperature and moisture relationships (Hitchcock, 1955), its geographical distribution (Wilkinson, 1970; Wharton, 1974; Knott, 1980) and its population dynamics (Sutherst et al., 1978). Free-living eggs and larvae are found in pastures and the parasitic stages feed on bovines.

TABLE I

Values of parameters constituting each CLIMEX index for the species used as examples. Temperatures are in degrees Celsius

Parameter	<i>B. microplus</i>	<i>R. appendiculatus</i> <i>A. variegatum</i>	<i>H. irritans exigua</i> (<i>H. irritans irritans</i>)
SM0	0.05	0.05	0.05
SM1	0.70	0.70	0.70
SM2	2.0	1.5	2.0
SM3	4.0	2.5	4.0
DV0	15.0	12.0	12.0
DV1	31.0	23.0	28.0
DV2	35.0	28.0	35.0
DV3	40.0	30.0	40.0
SMDS	0.35	0.35	0.20
HDS	0.0009	0.0065	0.005
SMWS	2.0	1.5	2.0
HWS	0.002	0.002	0.0008
TCS	20.0	30.0	12.0 (5.0)
HCS	0.00025	0.0001	0.0011 (0.0001)
MCS	0	0	1
THS	35.0	31.0	35.0
HHS	0.0015	0.0015	0.0014
DL	0.0	0.0	0.0

The optimal temperature for development of free-living stages is about 28°C, with lower and upper thresholds around 12 and 40°C, respectively. Relative humidities greater than 80% are necessary for egg survival. These observations were used as starting points to derive the parameter values (Table I) for the growth and stress indices. The values were systematically altered to give the best fit to the distribution of *B. microplus* in Queensland (Wilkinson, 1970; Knott, 1980). The tick's known relative abundance and reproductive performance in a wide range of locations in eastern Australia (e.g. Snowball, 1957; Harley, 1966; McCulloch and Lewis, 1968; Wharton et al., 1969; Sutherst et al., 1979; Mahoney et al., 1981; Johnston et al., 1981; Sutherst, 1983; R.W. Sutherst, unpublished data, 1983) were also used.

In Fig. 5, the observed distribution of *B. microplus* in Australia (Wharton, 1974) is compared with the predicted distribution based on the above CLIMEX parameter values. Global observations and predictions using the same CLIMEX parameter values are compared in Fig. 6.

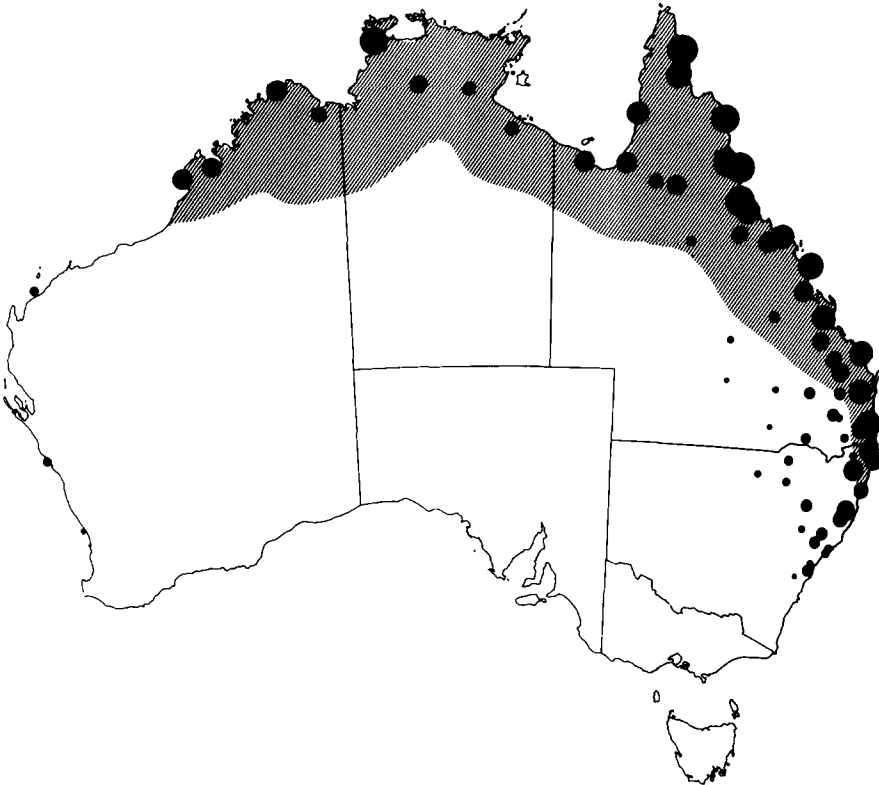


Fig. 5. The relationship between the distribution of *B. microplus* in Australia and the eco-climatic indices derived using the CLIMEX system described in the text. The areas of the circles are proportional to *EI*.

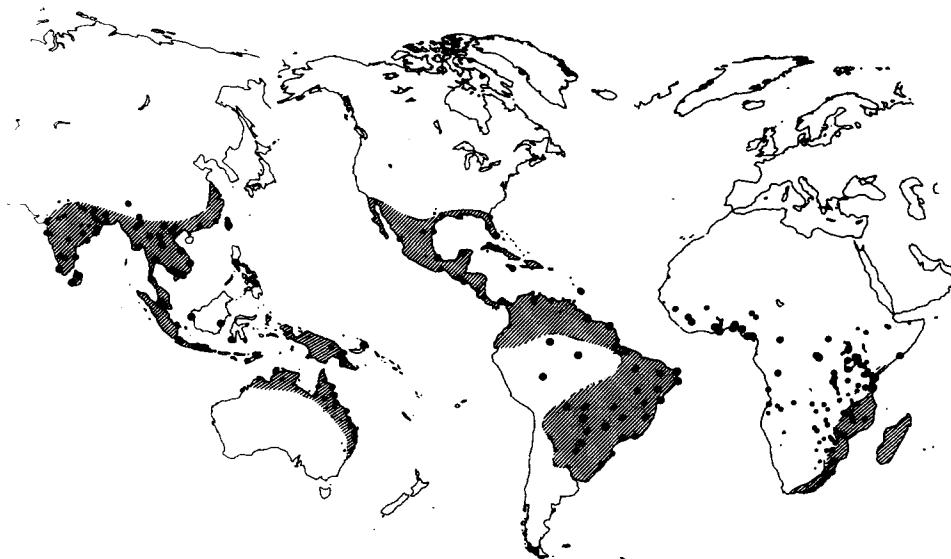


Fig. 6. Global predictions of *EI* superimposed on the global distribution of *B. microplus*. The areas of the circles are proportional to *EI*.

The global predictions correspond well with the observations which were not used to fit CLIMEX. They indicate, for example, that areas in which eradication has been successful in North America and in southern Argentina are less favourable climatically than many other parts of the world in which this species is a pest. Within Australia, the tick has the potential to persist well south of the tick quarantine area in the north-east of New South Wales.

Another interesting feature is the predicted favourability of south-east Asia and southern coastal Brazil. These areas are known to be favourable, the tick being a serious pest of *Bos taurus*-type cattle there. The discrepancy between indicated climatic favourability and observed scarcity of the tick on *Bos indicus* cattle reflects the known high resistance of such cattle to ticks (Wharton et al., 1969; Utech et al., 1978). The observed distribution of *Boophilus microplus* in Africa is also inconsistent with indicated climatic favourability. This is explained by its failure to colonise areas occupied by *B. decoloratus*, with which it produces sterile hybrid progeny (Spickett and Malan, 1978). Clearly areas such as western Kenya have a high risk from *B. microplus* if that species should be introduced there. These are the types of discrepancies which are useful as pointers to possible control measures and to the unrealised threats caused by some pest species.

CLIMEX can also be used to predict areas of enzootic instability of vector-borne diseases, and hence of clinical disease. For example, Babesiosis occurs in marginal areas with low *EI* values for *B. microplus*. Transmission is interrupted when vector populations are too small, leaving cattle exposed to infection at a greater age, when they are more susceptible. By selecting such

values, maps can be produced to show those areas most at risk from a given disease. Likewise, nutritional stress affects the ability of domestic animals to resist parasite attack. The dryness stress index (McCowan, 1980–81) describes the importance of nutritional stress in tropical areas.

(b) *Rhipicephalus appendiculatus* Neumann and *Amblyomma variegatum* Fabricius

The two companion species of ticks have similar distributions in East Africa (Yeoman and Walker, 1967; Walker, 1974). CLIMEX parameter values were systematically altered until they gave the best visual fit to the observed distribution and the relative abundance of the two ticks in Kenya as estimated from survey data by J.B. Walker, R.M. Newson and R.J. Tatchell (personal communication, 1983). Correlations between observers and between CLIMEX predictions and observers were all statistically significant and around $r = 0.5$. Predictions were then made for the rest of the world (Fig. 7). For *R. appendiculatus*, they correctly identified the south-eastern coast of S. Africa as being favourable (Howell et al., 1978) and indicated that other favourable areas exist in the Americas, Australia and Asia.

In addition, the prediction identified the Caribbean region as being moderately favourable, consistent with its successful colonisation by *A. variegatum*. They also demonstrated the high risk posed by that tick species to neighbouring countries. Note also that the predicted high favourability of South Africa and West Africa disagrees with the absence of *A. variegatum* in



Fig. 7. Predicted global EI values for *R. appendiculatus* and *A. variegatum*. The areas of the circles are proportional to EI.

the former and *R. appendiculatus* in the latter. These disagreements pose questions as to why the ticks are not in these areas, as there is no obvious physical barrier and their companion species is successful there. The answer in the case of *A. variegatum* is probably the occurrence of hybrid sterility between crosses of *A. hebraeum* and *A. variegatum* (Rechav et al., 1982), which appears to create a parapatric boundary in northern Zimbabwe (Norval, 1983). The absence of *R. appendiculatus* from W. Africa warrants study, particularly in view of likely increases in trade between East and West Africa.

(c) *Buffalo fly*, *Haematobia irritans exigua*

The buffalo fly, *Haematobia irritans exigua*, is of south-east Asian origin and was introduced into Australia in the late 19th century. It is closely related to the horn fly, *H. i. irritans*, which occurs naturally in northern Asia and Europe, and which was introduced into North America last century. The parameter values for CLIMEX were estimated from the distribution of the buffalo fly in Australia and extrapolations were made to other parts of the world. Of particular interest are the high predicted *EI* values for *H. i. exigua* in Africa, where dung beetles (Bornemissza, 1976) and predators (Wallace, 1979) have been collected for release into Australia. This biological control programme is based partly on the assumption that some areas of Africa are climatically favourable for *H. i. exigua*, and that the lack of pest status of the genus in Africa is due to biological rather than climatic or management factors.

The predictions in Fig. 8 are that the east coast of Africa and parts of



Fig. 8. Global map of *EI*'s for *H. i. exigua*. The areas of the circles are proportional to *EI*.

West Africa are highly favourable for *H. i. exigua* and, by inference, for the African representatives of the genus, particularly *H. thirouxi potans*. This prediction supports the view that *Haematobia*'s scarcity in Africa is due to factors other than climate.

(d) *Horn fly*, *H. irritans irritans*

Using the information on buffalo fly in Australia, some useful information was obtained on the horn fly in North America. Diapause enables the horn fly to survive much more severe winters than the buffalo fly. By incorporating a greater tolerance to low temperatures (low *CS*) in the buffalo fly parameters, estimates of *EI* for horn fly in North America were derived, as illustrated in Fig. 9. The predicted distribution and seasonal abundance closely match observations (e.g. Haufe, 1973; Kunz and Cunningham, 1977). Horn fly populations are highest in the south-east U.S.A. and lowest in northern and dry areas. The observed success of horn fly in tropical areas of N. America contrasts with its failure to colonise south-east Asia, where the buffalo fly is present. Once again, the observations deserve study to see whether hybrid sterility is involved and can be exploited for eradication or control of horn fly by summer release of buffalo fly in areas with cold winters.

The *EI*'s for horn fly in Europe are much less than those for North America (Fig. 9). The cause was explored by examining the mean population growth indices (*GI*'s) (Table II). They show that North America has far greater potential than Europe for propagation of horn fly populations in



Fig. 9. Global map of *EI*'s for *H. i. irritans*. The areas of the circles are proportional to *EI*.

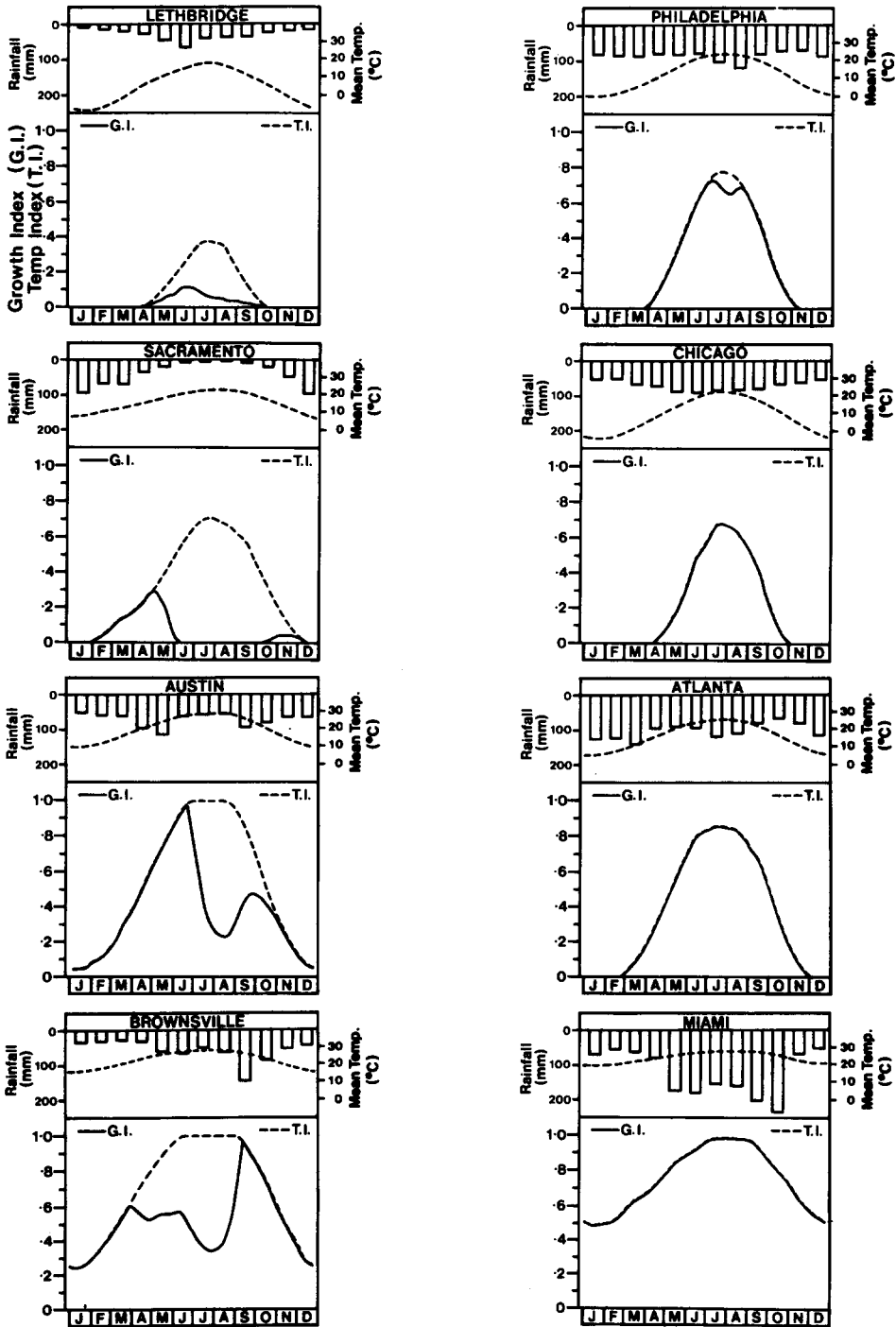


Fig. 10. Weekly *TI* (-----) and *GI* (—) values for *H. i. irritans* in North America. Mean monthly rainfall is shown as a histogram and mean temperatures as a broken line.

summer. Any decision to search for biological control agents in Europe must take this into account.

CLIMEX can also be used to explore the possible consequences of seasonal changes in favourability in different places. Weekly growth and temperature indices for *H. i. exigua* and *H. i. irritans* at selected North American sites are shown in Fig. 10. The graphs illustrate the probable timing, duration and extent of population changes in the different locations. The single, low curve for *GI* in Lethbridge agrees with the observations of Haufe (1973) and contrasts with the higher and broader curve for Austin, Texas, where a double peak occurs during the season (e.g. Bruce, 1964; Kunz and Cunningham, 1977). The graph for Austin suggests that the cause of the bimodal peak is climatic. The relative length of the favourable season at different locations is also shown by the time when *GI* values are greater than zero.

TABLE II

A comparison of selected mean weekly growth indices (*GI*) for the horn fly *H. i. irritans* in Europe and N. America

Europe		N. America	
Location	(<i>GI</i>)	Location	(<i>GI</i>)
Stockholm	3	Lethbridge	3
Moscow	6	Chicago	20
Munich	9	Philadelphia	26
Paris	7	Sacramento	6
Southampton	8	Austin	38
Rome	11	Houston	56
		Miami	75

(e) *South African biting fly, H. thirouxi potans*

CLIMEX can be used to compare the climatic favourability of different years in the same location. The fly *H. t. potans* occurs in the south-eastern and eastern coastal areas of South Africa. Although it is not usually a pest on cattle, there have been sporadic outbreaks, one of which occurred in the 1930's (Du Toit, 1938). During that outbreak, the fly caused severe problems as it moved up the coast and into Natal. CLIMEX was run with parameter values for *H. i. exigua* (i.e. no diapause) for three locations — at Port Elizabeth, East London and Durban along the east coast of South Africa (Fig. 11). The cold stress index shows that winters in the 1930's were much milder than in recent years at Port Elizabeth and Durban. Such information needs to be considered in any attempts to explain recent sporadic outbreaks of *H. meridiana* in South Africa (Newsholme et al., 1983) and the expansion of the distribution of buffalo fly in Australia in the 1970's and 1980's (Williams et al., 1985).

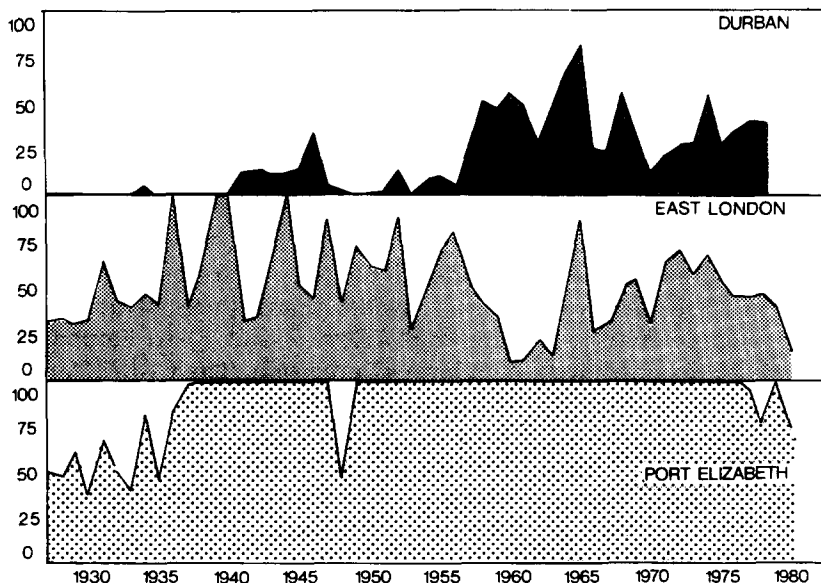


Fig. 11. Annual cold stress indices $\times 100$ (lethal temperature option) for *Haematobia* ($TCS = 12.0^{\circ}C$) in three coastal towns on the east coast of South Africa from the 1920's to 1980.

DISCUSSION

CLIMEX provides rapid, quantitative assessments of the climatic favourability of given localities and times for different species of arthropods. However, several limitations inherent in relating geographical distributions of animals to climate apply.

- (i) The distributions of some species are not determined by climate. As Krebs (1972) points out, the role of dispersal, behaviour and the influence of other species should be considered before assuming that climate is limiting.
- (ii) Some mobile insects annually recolonise areas in which a local population has failed to survive through the unfavourable season (i.e. where the product of the stress indices = 1) (e.g. Hughes, 1979). In such situations only the potential for the immigrants to propagate is of interest, and is described by the population growth index GI .
- (iii) Caution is needed to avoid drawing conclusions based on the distribution of an animal when that distribution has already been used to fit or modify CLIMEX parameters. Use of the model is valid only when comparing independent sets of data.
- (iv) We believe that the reliability of CLIMEX is more closely related to the accuracy and scope of the data used to derive the parameter values in the model than to the nature of the model. Use of long-term averages of climatic data have obvious limitations, but can be supplemented by

measures of variability of climate when detailed analyses are justified. Measured evaporation is preferable, as meteorological data are often weak for use in estimating evaporation. A specific need for caution arises when CLIMEX indicates that dryness is limiting, as the presence of local swamps often provides favourable habitats.

- (v) The ecoclimatic indices are more sensitive to extreme values than to intermediate values of the stress indices. To avoid undue confidence being placed in the precision of CLIMEX predictions, the index values have been presented on maps as a series of circles, the areas of which are proportional to the value of the index, rather than as precise numbers. In addition, simple functions were used (Figs. 2 and 3) to emphasise that the indices do not have a high level of precision. The CLIMEX program has been coded to facilitate imaginative alteration of the functions to suit particular user needs which will widen and extend the model's usefulness. The use of East Africa to derive parameter values for *R. appendiculatus* above illustrates how choice of a small area with complex topography can sometimes provide the wide range of parameter values desirable to fit CLIMEX.

By adjusting model parameters to match observed distributions, CLIMEX can be used to explore the animal's response to temperature and moisture. For example, the parameter values for the tick *Haemaphysalis longicornis* indicate that the species cannot tolerate mean ambient maximum temperatures much in excess of 26°C (G.F. Maywald and R.W. Sutherst, unpublished data, 1983). On the other hand, the parameter values may reflect the effect of climate on other aspects of the animal's life system, such as the nutritional value of pasture or the resistance of a host to parasite attack. Judicious use of CLIMEX can suggest the action of such factors. Discrepancies between observed and predicted distributions can be just as useful as agreements in identifying limiting factors.

Population size is not necessarily related linearly to the *GI* or *EI* for a number of reasons, including density dependence or cumulative population increase in multivoltine species. Detailed ecological studies and population models are needed to explore such relationships.

One constraint on the use of CLIMEX is the lack of information in the literature on the relative abundance of different animals in different environments. Much of the survey work on animals lists species as being merely present or absent during visits made in various seasons. Even crude estimates of the relative abundance of animals in different environments would be of great value.

In conclusion, we believe that CLIMEX serves a useful function in investigating the role of climate in the ecology of many animals. It is an exploratory tool which can be invaluable, particularly in considering problems relating to the introduction of species from one area to another, e.g. as occurred with the medfly, *Ceratitis capitata* (Weidemann), into California recently.

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