

Chapter 2

Temporal and spatial distribution of African Wild Silk Moth, *Gonometa postica*, eruptions in southern Africa

“In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be wholly accounted for by climatal and other physical conditions”

Charles Darwin (1859)

**Temporal and spatial distribution of African Wild Silk Moth, *Gonometa postica*,
eruptions in southern Africa**

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Abstract

The African Wild Silk Moth (*Gonometa postica*) experiences large inter-annual population size fluctuations in southern Africa. This species is currently of economic interest, as the focal species in the initiation of an African Wild Silk Industry. However, a consistent problem in the industry is the lack of a sufficient supply of cocoons. Therefore, we present data from three years of distribution surveys of eruptions of African Wild Silk Moths in southern Africa. Eruptions of the species show large degrees of variation on both spatial and temporal scales. In addition, we show an overall decrease in the persistence of eruptions over the sampling period. Furthermore, we use generalised additive modelling (GAM) to identify climatic variables that are significantly correlated with presence/absence of the species. Temperature and rainfall before the emergence of adult moths are significantly correlated with presence/absence. However, the effects of exogenous and endogenous factors on population cycles in this species are probably interlinked. Thus only long-term multidisciplinary population dynamics research will be sufficient to address the factors responsible for the complex population cycle observed in this species.

Keywords: distribution, generalised additive model, cyclical species

Introduction

The African Wild Silk moths (*Gonometa* spp., Lasiocampidae) are species that are presently of particular economic interest in southern Africa. The Liberty Life International Wild Silk Workshop held in Pretoria (4-5 November 2002) bears testament to the level of interest both in southern Africa and abroad. Both *Gonometa postica* and *G. rufobrunnea*, two species of African Wild Silk moth native to southern Africa, have been shown to possess a silk fibre of exceptional quality (Freddi *et al.* 1993, Akai *et al.* 1997) and attempts have already been made at initiating an industry for the utilization of *Gonometa* cocoons in the production of African Wild Silk. Such an example is Shashe Silk Pty (Ltd) in northwest Botswana. Shashe silk plummeted due to an insufficient supply of cocoons for the production of silk. The failure of Shashe Silk was the result of an incomplete understanding of the biology of the species and secondly, poor business management (McGeoch 2002). Shashe Silk ignored the cyclical nature of the species, and the lack of eruptions resulted in an unbalanced expenditure versus crop value ratio. Currently, several small-scale cottage industries are utilizing *Gonometa* fibres to weave a variety of textile products. Although these industries have been successful in utilizing *Gonometa* cocoons, a consistent complaint is the lack of a sufficient supply of cocoons. To this end a joint venture between the North West Provincial Government and the Council for Scientific and Industrial Research, called Wild Silk Africa, has been established in Ganyesa, north of Vryburg, in order to aid in the collection of cocoons and provide local communities with a source of revenue. However, such an industry cannot be based in a single region due to the cyclical and patchy nature of the population eruptions.

The *Gonometa* species in southern Africa have been shown to exhibit large inter-annual population fluctuations (Veldtman 2005). However, it is uncertain whether eruptions are only the result of local populations experiencing ideal conditions or whether current eruptions are initiated by dispersal of individuals from eruptive populations in previous generations. A second observation, regarding eruptions, is that they are patchily distributed at both the local and regional scale (Veldtman 2005). *G. postica* has a complex population cycle that is characterized by two generations per annum, the first starting in September-October when adult moths emerge from cocoons. Adults lack feeding mouthparts and survive for three to five days (Hartland-

Rowe 1992), during which breeding occurs. Eggs are laid, larvae emerge and pass through six instar larval stages in approximately five weeks, after which the larvae construct cocoons, pupate and enter a period of diapause. This period of diapause either carries through to the following September when adults emerge, or is broken in February with adult emergence and an additional population cycle. Typically, this second generation comprises between 12-50% of the first generation (Hartland-Rowe 1992), and culminates in pupae that emerge as adults in September. The contribution of this second cycle to eruptions of the species is unknown, and is necessary to consider in relation to other endogenous and exogenous factors.

In particular, the influence of exogenous factors, such as climate, on eruptions is necessary to understand before it can be determined whether cocoons are a sustainable resource for the African Wild Silk industry. Since it has been suggested that the patchy nature of *Gonometa* eruptions may be the result of spatial correlation in climatic variables (Veldtman 2005), we investigated the temporal correlation of rainfall and persistence of eruptions. Two main hypotheses, relating to climate, have been suggested. Firstly, some have noted the incidence of eruptions following periods of drought (Hartland-Rowe 1992). A putative explanation for this observation is the reduction of numbers of dipteran and hymenopteran larval parasites. Supposedly, a reduction in parasite numbers due to unfavorable conditions allows *Gonometa* populations to reach eruptive proportions. Secondly, large population crashes may be the result of heavy rainfall that causes high early instar mortality (Hartland-Rowe 1992). This hypothesis is supported by observations of low population sizes at sites that had experienced exceptionally heavy summer rainfall (Veldtman 2005). The purpose of this manuscript is to report on temporal variation in presence/absence of *G. postica*, and to address the influence of climate, in particular rainfall and temperature, on the distribution of eruptions over a three-year sampling period. Our results indicate a decline in eruptions over the sampling period, and furthermore statistical correlation of rainfall and temperature at the time of moth emergence with presence/absence.

Methods and materials

Distribution data collection

The purpose of this study was to assess the distribution of first generation *G. postica* eruptions across southern Africa for a period of three years (2002-2004). *G. postica*

experiences a period of suspended development or diapause during the winter months in southern Africa (May – August). Therefore, we surveyed the Kalahari region of southern Africa (Figure 1) on an annual basis (2002-2004) for the presence/absence of *G. postica* cocoons on *Acacia erioloba*, *A. tortilis*, *A. mellifera* and *A. haematoxylon* trees. We drove approximately 10 000km along roads in the Kalahari, stopping every 50km and checking for the presence or absence of cocoons. Although we only stopped every 50km, it is easy to spot cocoons whilst driving due to their size and conspicuousness. The larvae of *G. postica* are moderately polyphagous (Veldtman 2005), feeding on the leaves of two angiosperm families (Mimosaceae and Caesalpiniaceae). Although, we only intended to check for presence of cocoons on the *Acacia* species, it was nonetheless easy to spot cocoons on other species, such as the alien *Prosopis glandulosa*. Both the presence and absence of cocoons were recorded along with GPS reading of each locality, for each of the survey years. We drove the same route in 2002 and 2004, and a shorter route in 2003. Therefore, temporal changes in the presence/absence of eruptions do not represent un-sampled localities, but rather a true change in presence/absence of eruptions.

Climate data collection

Climate data, including total monthly rainfall and average monthly temperature, for the period 2001-2004 were obtained from the South African Weather Service. Data from a total of 167 rainfall and 35 temperature stations, distributed across the Northern Cape and North West provinces (Figure 1), were utilised in subsequent analysis. However, since these climate stations did not overlap with distribution presence/absence sampling localities, it was necessary to construct climate surfaces using interpolation techniques. We used an Inverse Distance Weighted interpolation procedure (power = 2, search radius = variable, number of points = 12) implemented in the spatial analyst extension of ArcGis 9 (www.esri.com). Thereafter, rainfall and temperature values were calculated, from these interpolated surfaces, for each of the presence/absence distribution localities surveyed, in each of the sampling years (2002 – 2004). Climatic variables (predictors) used in the distribution modelling were chosen so as to be informative with regard to the species' life cycle. The principal host species, *A. erioloba*, experiences a leaf flush in September. The timing of bud-burst is critical for many insects, with many insects exhibiting synchrony of egg laying and host-plant bud-burst (Dixon 2003). Therefore, the relationship between climatic factors and host-plant leaf flush, and the synchrony of egg laying by female

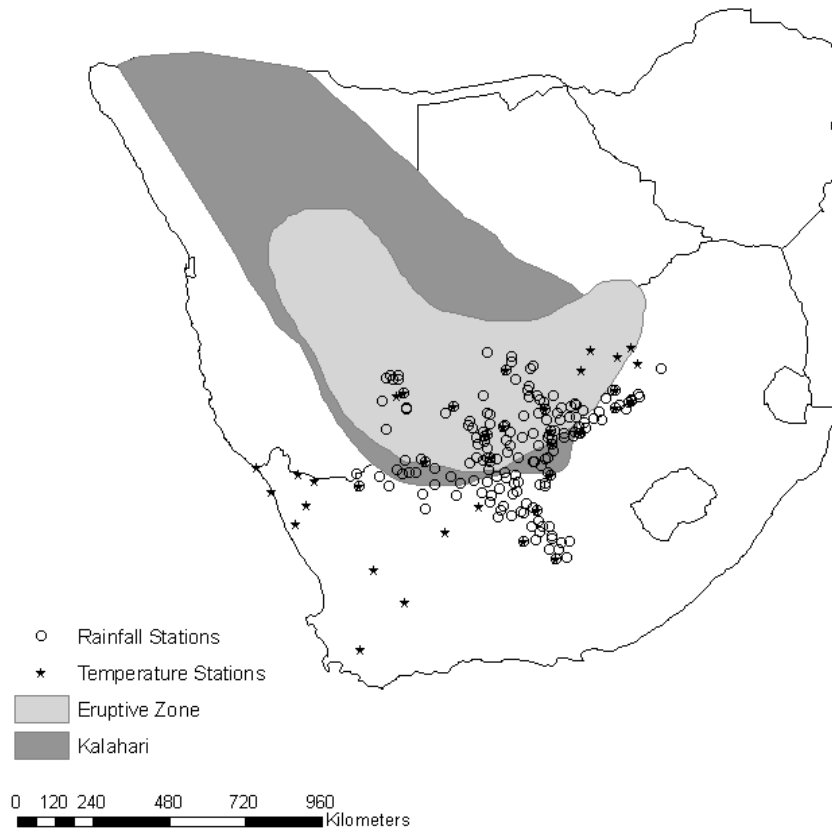


Figure 1: Distribution of rainfall and temperature weather stations used for the calculation of interpolated climate surfaces. The extent of the eruptive zone and distribution of the Kalahari biome in southern Africa is also shown.

G. postica moths may be important in the persistence of local populations. Climatic variables that were considered of importance for this study were (i) pre-emergence rainfall and temperature, (ii) rainfall and temperature during larval development, and (iii) rainfall and temperature coinciding with the second generation (Table 1). As a result of the long pupal diapause, presence/absence response variables from any year is directly related to the larval development and pupation success of the previous year. These variables were therefore used as predictors of species distribution in the subsequent predictive distribution modelling (Table 1). All ArcGis 9 analysis utilized the GCS_Hartebeeshoek_1994 geographic coordinate system.

Distribution modelling

The purpose of the distribution modelling was to determine which of the climatic predictor variables were correlated with presence/absence data (i.e. response variables) collected from 2002-2004. Although it is not possible to determine causation from correlation (Sokal & Rohlf 1981), this approach still allows a statistical description of functional relationships between environmental and response variables. We used a generalized additive model (GAM), which is a special semi-parametric case of the generalized linear model (GLM), that allows regressions to be estimated for non-standard distributions (Poisson, binomial, gamma), and allows better fitting of species response curves to environmental gradients (Austin 2002). Specifically, we use the GRASP package (Lehmann *et al.* 2002) implemented in the R statistical language (R Development Core Team 2005). The modelling approach was subdivided into three steps; (i) data exploration, (ii) model selection, and (iii) model interpretation. Firstly, exploratory analyses were conducted to describe the environmental space occupied by the species, and to detect statistical correlations between variables. In the former we plotted histograms of distribution data with respect to the environmental variables they represent. Correlated predictor variables may be problematic in the estimation of additive surfaces (Lehmann *et al.* 2002) and therefore we identified variables that were strongly correlated. Secondly, model selection was performed, under a quasi-binomial model, through a stepwise procedure that selects significant predictor variables. The process begins with a starting model, and then eliminates climatic predictors on the basis of whether the predictor provides a significantly better fit (ANOVA) to the observed data than a model without the current predictor. Finally, we used response curves to ascertain how presence/absence is related to the environmental predictors.

Table 1: Climatic predictors and response variables used to model the distribution of *Gonometa postica* eruptions. JAS = July – August – September, OND = October – November – December, JFM = January – February – March. *Data unavailable for this study.

	Presence/absence		
	2002	2003	2004
Temperature (average monthly - °C)			
Pre-emergence (T_{pe})	JAS 2001	JAS 2002	JAS 2003
Larval development (T_1)	OND 2001	OND 2002	OND 2003
Second generation (T_2)	JFM 2002	JFM 2003	JFM 2004
Precipitation (total - mm)			
Pre-emergence (P_{pe})	JAS 2001	JAS 2002	JAS 2003
Larval development (P_1)	OND 2001	OND 2002	OND 2003
Second generation (P_2)	JFM 2002	JFM 2003	JFM 2004*

Results

Distribution results

The survey of first generation cocoons conducted in the July 2002 indicates the patchy nature of eruptive populations in *G. postica* (Figure 2a). Sampling effort during 2003 (Figure 2b) was less intense and at a smaller geographic scale, yet the intensity at this reduced scale was equivalent to that of 2002. A general observation from 2003 distribution data is the observation of clusters of presence and absence data (Figure 2b). Furthermore, comparatively fewer presence localities were found versus that in 2002 (Table 2). The reduction in the number of eruptions in 2004 is even more severe (Table 2, Figure 2c) with even fewer presence localities recorded, and sampling effort equivalent to that of the 2002 survey.

Modelling results

Exploratory analysis of the predictor and response variables indicated a low incidence of presence samples (Figure 3, Table 2). Presence samples are, however, clumped in the distribution of pre-emergence temperature (Figure 3a). Correlations between variables indicate that most variables are correlated, as one would expect for climate data. However, no two variables have r , the correlation coefficient, greater than 0.80. Therefore, all variables were retained for the model selection process. Stepwise selection of statistically significant climatic predictors for the distribution of *G. postica* identified the following model:

$$Y = s(T_{pe}, 2.605) + s(T_2, 1.009) + s(P_{pe}, 4.391)$$

where Y = response variable, i.e. presence/absence, s = smoothing coefficient, and predictor variables are as in Table 1. Two variables, temperature (T_1) and precipitation during larval development (P_1) were not selected as contributing significantly in the model selection procedure. Finally, response curves of three predictor variables included in the model indicated the relationships between predictor and response variables (Figure 5), i.e. the species distribution. Response curves for temperature and precipitation before the emergence of adult moths are complex and clearly not linear relationships. Indeed, precipitation before emergence (P_{pe}) indicates that intermediate total precipitation over the three-month period (July – September) is likely to result in fewer eruptions. However, both low and higher levels of precipitation at this time

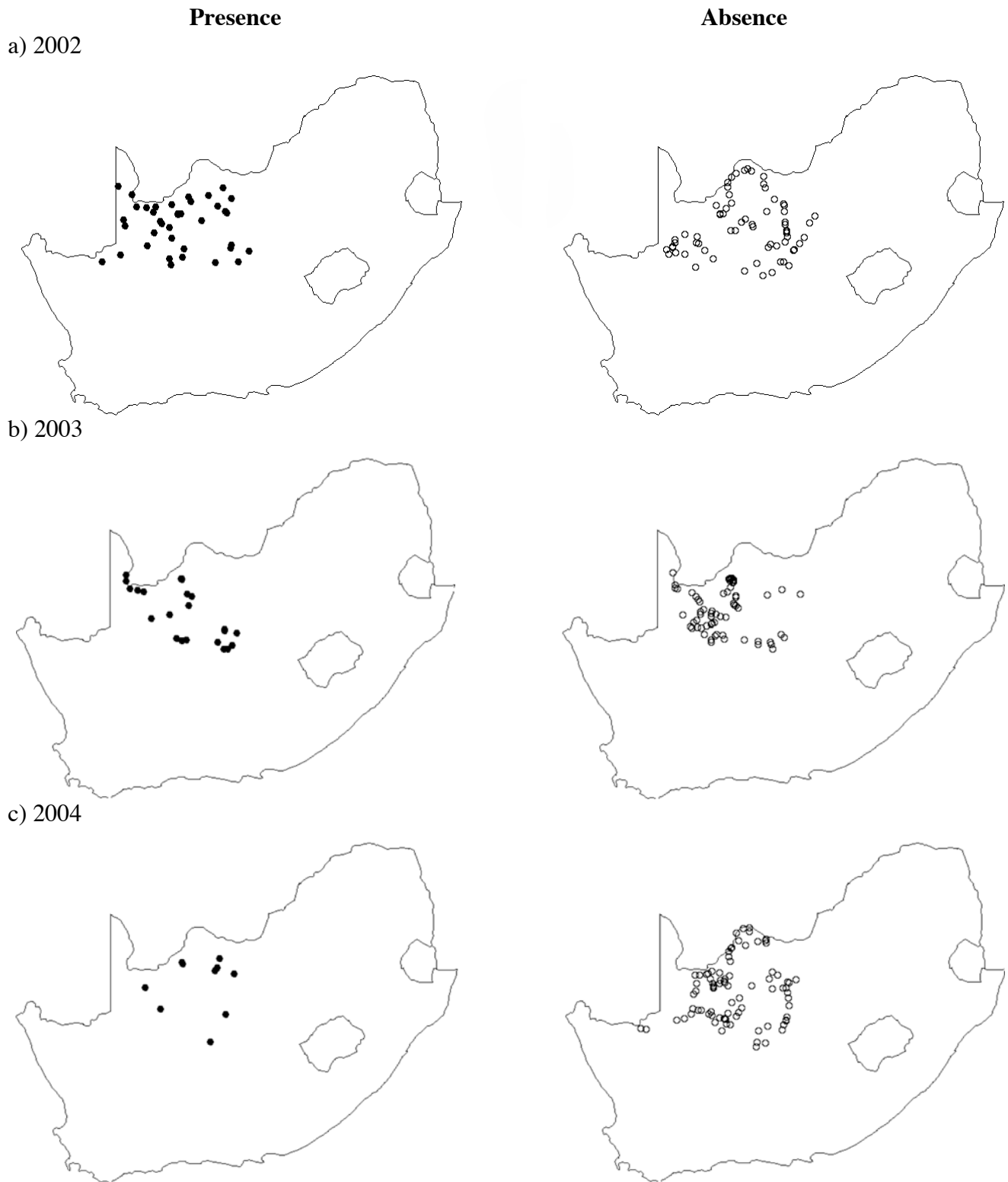


Figure 2: Temporal change in presence and absence of *G. postica* eruptions as determined with annual surveys from 2002-2004.

Table 2: Total number of sampled sites and proportion of presence sites of all sites sampled during 2002, 2003 and 2004.

Sampling year	Total sites sampled	Proportion presence
2002	185	0.42
2003	98	0.25
2004	200	0.07

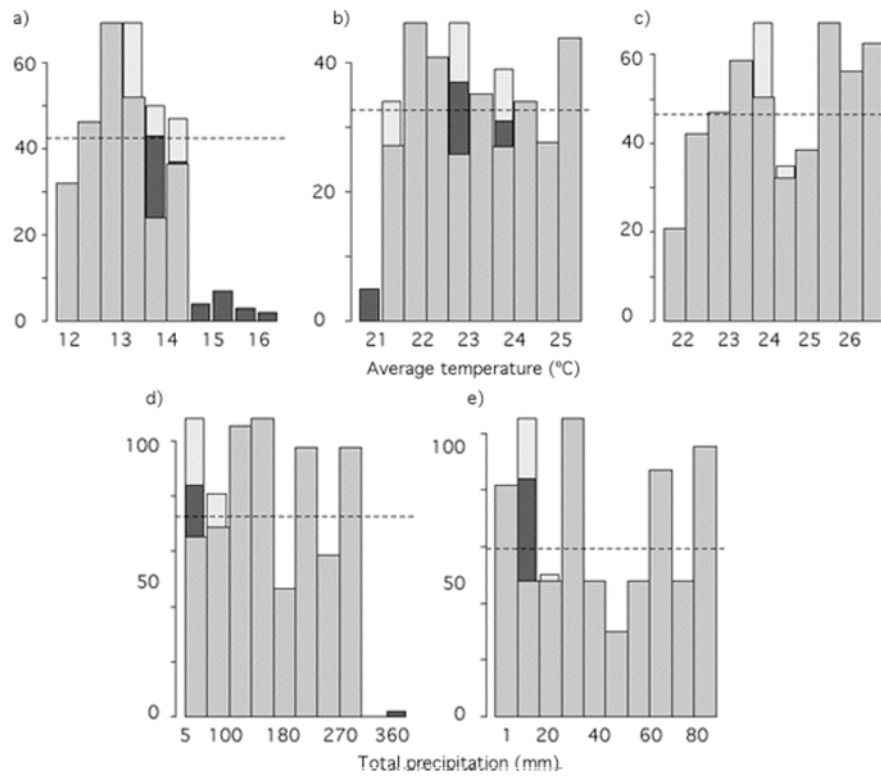


Figure 3: Distribution of environmental predictors and the occurrence of presence/absence samples. Histogram bars represent the distribution of both presence and absence samples, where dark areas are the distribution of presence samples. a) T_{pe} - Pre-emergence temperature, b) T_l - larval development temperature, c) T_2 - Second generation temperature, d) P_{pe} - Pre-emergence precipitation, e) P_l - larval development precipitation.

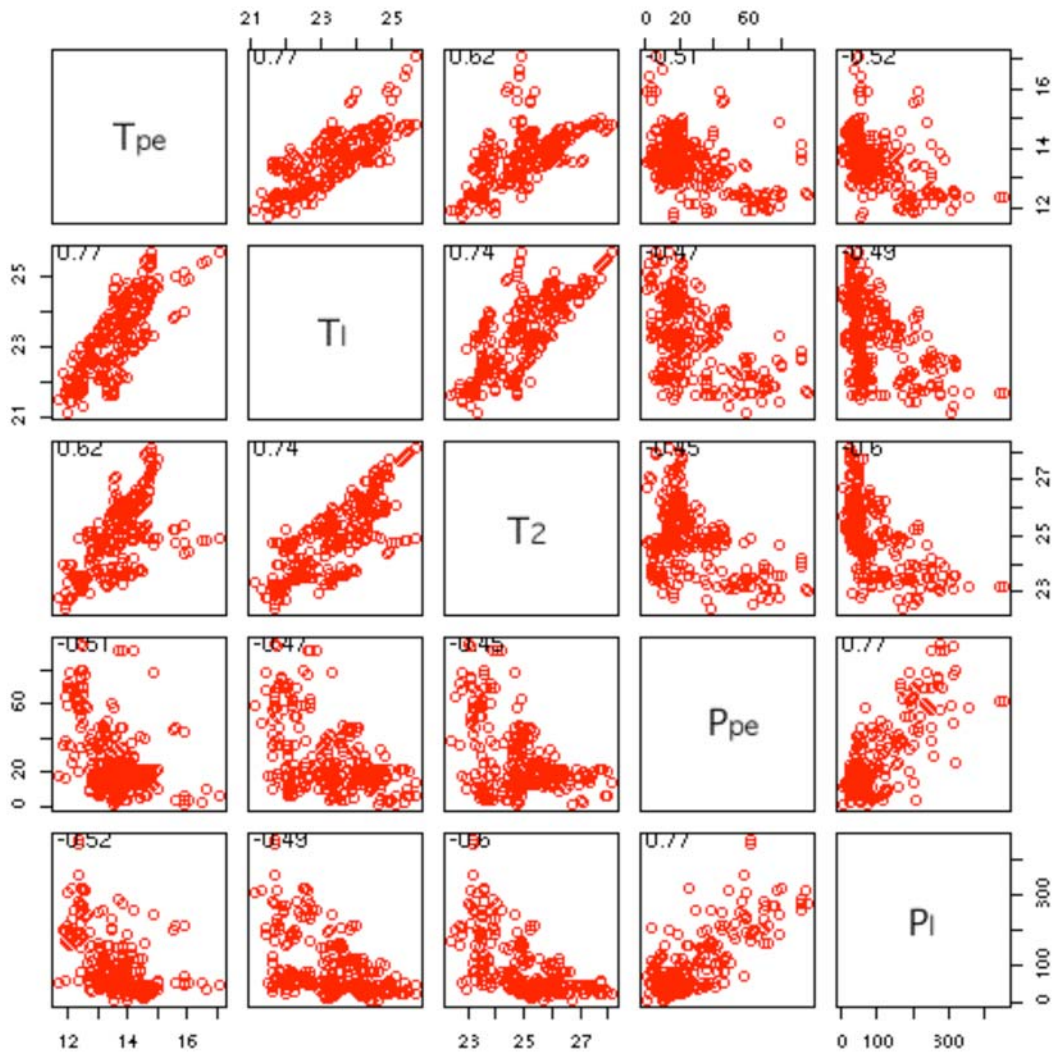


Figure 4: Statistical correlations between pairs of climate predictor variables used in the GAM model. Climate variables are named as in Table 1.

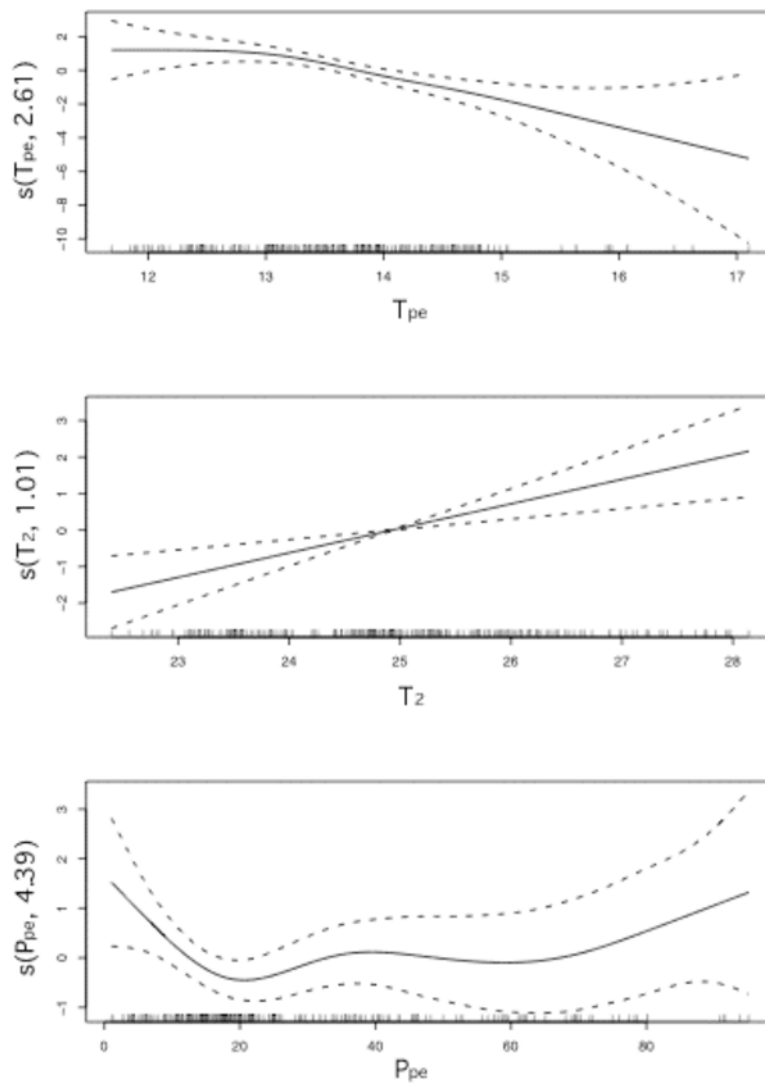


Figure 5: Response curves of predictor variables in selected generalized additive model (GAM). In each case the relationship between the predictor variable and its implementation in the model is represented. Predictor variables are named as in Table 1.

seem to be correlated with presence of the species. Lower temperatures before emergence are correlated with presence of the species (Figure 5), yet response curves for temperature during the second generation suggests the inverse of this relationship. Although, some of the results seem contradictory, the current model does provide a framework for future work and discussion.

Discussion

The distribution of *G. postica* clearly shows a pattern characteristic of an eruptive species, with little temporal consistency in population eruptions. Of particular interest in this study are (i) the temporal decline in *G. postica* eruptions, (ii) the degree of patchiness and the persistence of these patches, and (iii) the correlation of presence/absence with environmental variables. Firstly, we observed an overall decline in the presence of *G. postica* cocoons over the three years sampled in this study. Although, sampling effort was not consistent over the three years, with less sampling in 2003, these results are still evident in the proportion of presence localities observed relative to the total number of localities sampled (Table 2). We found pupae in approximately 42% of sampled localities in 2002, yet only 7% of the sites sampled in 2004 had pupae present. This represents a considerable decrease in population size, and highlights the unpredictable nature of this species. The degree of spatial and temporal heterogeneity in this species is severe. These results are supported by previous work, where temporal *G. postica* pupal abundance at local sites was shown to range across two orders of magnitude (Veldtman 2005). However, some areas do appear to have eruptions that have persisted over time (Figure 2). The correlation of these clusters of presence data with environmental variables was explored using generalized additive modelling (GAM). The selected model included precipitation and temperature before the emergence of adult moths as important determinants of presence/absence. These results are intuitive, since it is thought that temperature acts as a cue for the termination of diapause in this species (Hartland-Rowe 1992), and secondly, since total precipitation at this time may be important in determining foliage quality of the host species, at the time of its leaf flush. The results presented here, however, do not suggest causal relationships, but are merely correlations. Therefore, it would be necessary to conduct further studies investigating the relationships between these climatic variables and both silk moth population dynamics and host plant phenology. Although this model needs to be tested with additional data and validated

using cross-validation procedures (Fielding & Bell 1997), we do believe the approach followed here will assist in understanding the cyclical population dynamics of this species.

Several insect species have such population cycles characterized by large eruptions and population crashes (Turchin 2003). Examples that have been well-studied include the Larch budmoth, *Zeiraphera diniana*, (Bjornstad *et al.* 2002), southern Pine beetle, *Dendroctonus frontalis*, (Reeve *et al.* 1995), the desert locust, *Schistocerca gregaria* (Cheke & Holt 1993) and locally the armoured bush cricket, *Acanthopplus discoidalis*, (Holt *et al.* 2003, Minja & Green 2003. Turchin (2003) notes that the dynamics of such complex population cycles are attributed to the interaction between endogenous and exogenous factors. These factors encompass environmental effects, including climatic factors, population-specific effects such as density dependence and inter-species interactions, such as predator-prey relations. The overall decline in population eruptions of *G. postica* over the three sampling years in our study suggest that broad-scale spatial synchrony in population dynamics is evident in this species. Since dispersal, interspecific interactions (parasitism) and environmental variables are likely to influence the degree of spatial synchrony (Peltonen *et al.* 2002), it is difficult to determine whether the observed patterns are truly environmental. For instance broad scale patterns in rainfall might increase spatial synchrony, yet heterogeneity in the distribution of larval parasites might decrease spatial synchrony. Indeed Veldtman (2005) has detected some degree of spatial heterogeneity in the incidence of larval parasitism of *G. postica* at the local scale (100 trees), yet the inferred degree of heterogeneity was largely dependent on the spatial method used to quantify it. Spatial heterogeneity in larval parasites, and the influence of broad-scale climatic factors would tend to decrease and increase the degree of spatial synchrony in abundance, respectively, and thus complicate the inference of the effects of either factor in isolation. In addition, dispersal ability is likely to determine the scale at which spatial heterogeneity in abundance occurs, since adult mated female dispersal can seed the eruptions of subsequent years.

Therefore, it is imperative that several local *G. postica* populations should be monitored on an annual basis. Such local monitoring would include statistically rigorous estimates of abundance as suggested by Veldtman (2004), the collection of temporal life-history data, the direct estimation of dispersal ability with capture-mark-

recapture techniques, and the delineation of energetic requirements, in terms of foliage quality and quantity, of larvae to complete development. At the regional scale we propose the continued survey of both presence and absence distribution data, combined with abundance estimates at each site. These data combined with regional climatic information will allow the identification of climatic influences of *G. postica* eruptions. Given that some insect population cycles can occur on the order of 5-10 years (Turchin 2003) it is of utmost importance that these data are collected in a standardized manner over a long-time period. With the use of such long-term data we look forward to the development of population dynamics models that will allow the understanding of complex cycles in this species, and potentially enable the prediction of eruptions.

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