

Can observation of climatic variables be used to predict the flight dispersal rates of *Prostephanus truncatus*?

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- Abstract**
- 1 Attack by *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) on the maize and cassava stored by small-holder farmers in Africa is sporadic, varying considerably within and between years. The risk that food in store will become infested is related to the number of beetles dispersing by flight. A means of predicting years with high dispersal rates is needed to warn farmers when to be vigilant.
 - 2 The relationship between climatic variables and pheromone trap catches was observed in a forest-savannah transition zone in Ghana. These observations were used to devise a model using a mix of biological and empirical rules that operate on temperature and humidity data. The predicted and actual trap catch deviated by only +5% to –1% in years when there were high dispersal rates.
 - 3 The first part of the model estimates the numbers of beetles with potential for dispersal. The second part predicts the proportion likely to disperse. This is based on the apparent effect that those *P. truncatus* developing under low temperature conditions (about 24 °C) have a lowered propensity for flight, a response previously observed in a related species.
 - 4 The model was validated using climate data and trap catches from a woodland-savannah zone and a short grass steppe zone. With minor adjustment, the model worked well for these two habitats.

Keywords Farm storage, flight activity, risk assessment, pest management, rule-based model.

Introduction

An ability to predict the risk of serious pest attack is an important goal in agriculture (Nieminen *et al.*, 2000) and forestry (Ravlin, 1991) and enables increasingly targeted and effective control measures. This approach would be of value in the case of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) a serious beetle pest of the maize and cassava stored by small-holder farmers in Africa and Central America (Hodges, 1986; Markham *et al.*, 1991). Besides attacking stored food, the pest has large populations in the natural environment where its main host is believed to be dead wood (Nang'ayo *et al.*, 1993). Monitoring the incidence of *P. truncatus* using pheromone-baited flight traps has shown that the number of beetles trapped varies considerably between seasons and years in Mexico (Rees *et al.*, 1990),

Kenya (Giles *et al.*, 1995) and Benin (Borgemeister *et al.*, 1997a). Furthermore, it has been shown that there is a significant positive correlation between trap catch and the likelihood that stored food becomes infested (Birkinshaw *et al.*, 2002). This indicates that traps give an effective measure of the dispersing population that threatens stored food, although this population is skewed by sex, because 60–70% is female (Hodges *et al.*, 1998; Scholz *et al.*, 1998), and by age, because young beetles are more likely to fly and are more active fliers (Fadamiro, 1996; Scholz, 1997). However, pheromone traps are expensive and time consuming to deploy so their long-term use by extension services in developing countries is unlikely to be sustainable. As an inexpensive alternative, the current study set out to test whether climate data could be used to predict years when dispersing *P. truncatus* are particularly abundant.

Climate may have an effect on the abundance of dispersing *P. truncatus* in both the long- and short-term. Dispersal of *P. truncatus* is believed to result from crowding and degradation of food resources (Fadamiro & Wyatt, 1995;

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Scholz *et al.*, 1997). The rate of insect development and consequently the rate of population growth is affected by long-term climatic conditions. In the laboratory, the optimum conditions for development of the pest on maize are 32 °C and 70–80% relative humidity (RH), when the life cycle can be completed in about 27 days (Subramanyam & Hagstrum, 1991); adults live at least 4 months (Guntrip *et al.*, 1996). Humidity effects on development appear to be nonlinear with a more or less on/off response whereas temperature effects are more or less linear (Meikle *et al.*, 1998). In the short term, climate has a direct effect on the propensity of insects to disperse by flight. Fadamiro & Wyatt (1995) observed an optimum temperature for flight in the range of 25–30 °C, a nonlinear response, and a progressive (linear) increase in flight as RH rose from 25% to 50% to 75%, although differences were not statistically significant.

Several authors have used multivariate analysis to investigate the relationship between climatic variables and *P. truncatus* trap catch (Tigar *et al.*, 1994; Giles *et al.*, 1995; Nang'ayo, 1996). However, where predictions have been made, they have been very different in scale from observed catches. Farrell (2000) notes that their main use may lie in predicting relative rather than absolute abundance. Very recently, a study of flight activity in south Benin (Nansen *et al.*, 2001) identified day length, minimum RH and minimum temperature as important variables for predicting *P. truncatus* trap catch, offering some improvement on earlier attempts to predict trap catches.

The current study sought a means of predicting years when dispersing *P. truncatus* are particularly abundant. The first step was to examine the association between climatic variables and observed seasonal and annual variations in *P. truncatus* trap catch of a tropical rain forest-savannah transition zone in Ghana. The second step was to devise a rule-based model from this association and prior knowledge of the pest's biology. The use of such models in pest management has been discussed in detail by Holt & Day (1993). The model was subsequently validated with climate data and trap catches from two semi-arid areas.

Materials and methods

Procedures adopted for Hohoe/Ho

Pheromone trapping was undertaken at Hohoe (Table 1), in a tropical rain forest-savannah transition zone of the Volta

Region in Ghana and climate data collected from the Meteorological Station at Ho about 45 km south of Hohoe; the climate of the two towns is similar. At Hohoe, trapping was undertaken in five villages close to the town using Japanese beetle traps (Compton *et al.*, 1997) following the procedure described in Birkinshaw *et al.*, 2002). In each village, four traps were hung from trees about 1.5 m from the ground, with approximately 100–150 m between traps. Traps were emptied and pheromone capsules changed on a 2-weekly routine over a period of 5 years (1996–2001). For logistical reasons, trapping was discontinued on four short occasions.

The Ho Meteorological Station provided daily maximum and minimum temperature (mercury thermometers), daily rainfall, daily windrun expressed as cumulative wind in km/h measured from 9 hours to 9 hours using a mechanical anemometer, and RH (wet and dry bulb thermometers). For purposes of comparing trap catch and climate data, comparisons were made with humidity at mid-day and mean temperatures calculated from the daily maxima and minima. This method of calculating the mean temperatures is convenient but the values may be somewhat different from the true mean. To observe what differences there might be during the course of a year, hourly temperature data were collected by an electronic thermohygrograph (Temperature and Humidity Recorder model CT 485RS, Omega Engineering Inc., Stamford, CT, USA) located at the laboratories of the Ministry of Food and Agriculture in Ho. The temperature and humidity sensors were placed in a ventilated polystyrene box suspended in the shade just below the eaves of a building. Data from 6 days of the month, spaced more or less evenly, from February 1999 to January 2000, were analysed. The averages from hourly observations through out the day were then compared with those derived from maxima and minima.

Analysis of data

The initial analysis was used to explore the relationship between trap catch and climatic variables. An informal approach was chosen due to the nonlinearity of the effects of temperature and humidity on development and flight activity. Linear regression and CUSUM analysis (Oakland, 1987) were used, the latter to provide a clear view of when changes in conditions and in trap catches occur. The technique involves calculating the deviation of values from their

Table 1 Locations used for trapping *Prostephanus truncatus* and collection of climate data

Trapping location	Vegetation type (US Central Intelligence Agency, 1997)	Meteorological station	Trap type and frequency	Duration and no. of trapping periods
Hohoe, Ghana (7°19'N, 0°27'E)	Tropical rain forest – savannah transition	Ho (6°45'N, 0°35'E)	Japanese beetle trap – 14 days	January 1996 to September 2001 129 trapping periods
Nkwanta, Ghana (8°16'N, 0°31'E)	Deciduous woodland savannah	Kete Krachi (7°8'N, 0°0'E)	Japanese beetle trap – 14 days	January 1997 to July 1999 66 trapping periods
Morogoro, Tanzania (6°47'S, 37°43'E)	Short grass steppe	Kilosa (6°47'S, 37°02'E)	Delta (sticky) trap – 28 days	September 1997 to December 1999 24 trapping periods

average over the years and presenting a plot of cumulative deviation:

$$S_r = \sum_{i=1}^r (x_i - \bar{X})$$

Where S_r is the CUSUM score, x_i is the result from the individual sample i , \bar{X} is the mean of all samples for the period in question.

The technique is well known in process control and is very powerful for the detection of trends. When looking at CUSUM plots, the absolute values are not important, the slope of lines conveys the meaningful information. In this case, CUSUM plots enabled easy comparison between years and gave clues to the relationship between some variables.

The explorative analysis was tested by the development of a rule-based climate model, to predict *P. truncatus* trap catch, on an Excel spreadsheet. Rules were developed from observation of the relationship between trap catch and climatic variables in Hohoe and Ho, respectively, and prior knowledge of the biology of the pest.

Procedures at other locations

The rule-based model was validated on trap catch and climate data from two other locations in different agro-climatic zones, Nkwanta in Ghana and Morogoro in Tanzania (Table 1). In Nkwanta, four Japanese beetle traps

were located in each of five villages and the procedure was the same as in Hohoe. Climate data was collected at the Kete Krachi Meteorological Station, about 40 km from Nkwanta, in the same manner as Ho. At Morogoro, single traps were located at nine sites and most were within 20 km of the Kilosa Meteorological Station (Table 1) which collected climate data similar to that in Ghana, except that only humidity at 15.00 hours was available and so had to be used in the model. There were two important trapping differences from Ghana, delta traps (Hodges & Pike, 1995) were used instead of Japanese beetle traps and these were emptied monthly (Table 1).

Results

Observations Ho/Hohoe Volta Region Ghana

In Hohoe, the typical annual pattern of *P. truncatus* trap catch was two distinctive peaks, one during the Harmattan period (December to February) and the other 'Mid-year' (May to August) (Fig. 1). In 1998/99, the two peaks were not clearly defined and, instead, one massive peak arose from December through to July. In 1999/00, there was a massive Harmattan peak but a much reduced Mid-year peak. Compared with 1996/1997, catches in 1997/1998 and 1998/99 were 1.4- and 4.0-fold greater, respectively. Over a period of 5 years, abundance in dispersal varied greatly, offering an opportunity to deduce which factors influence trap catch. Preliminary analysis of the data suggested that

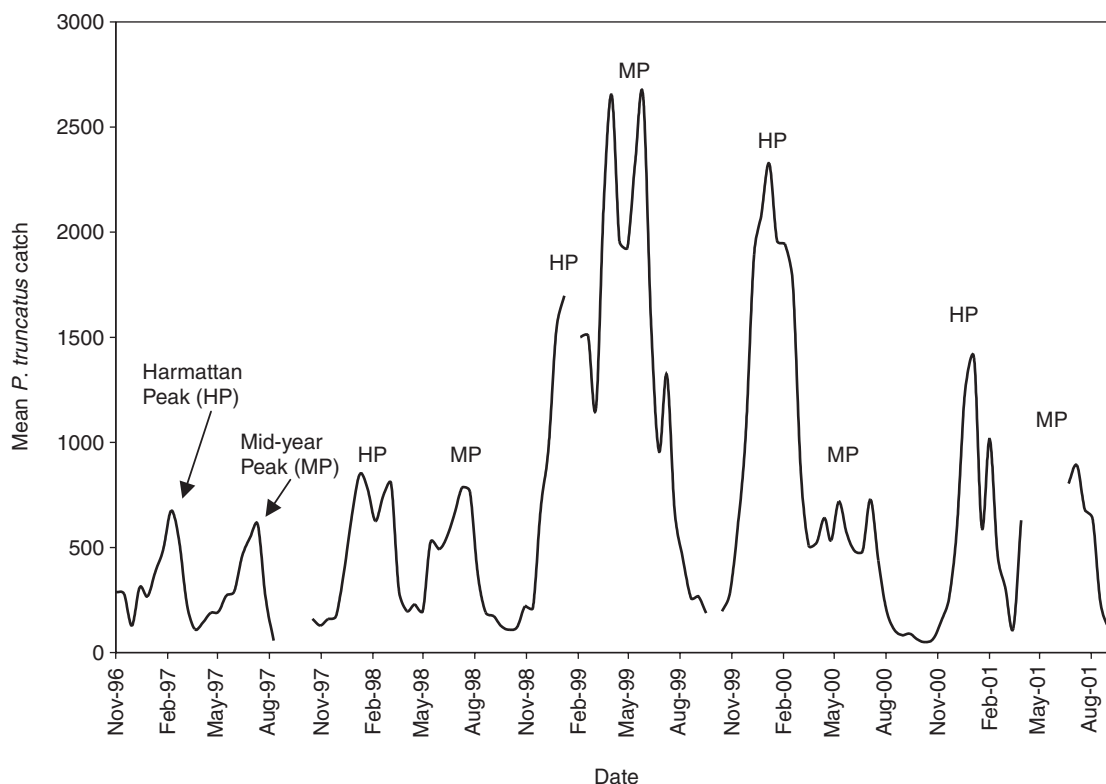


Figure 1 Annual variation in *Prostephanus truncatus* trap catch in five villages close to Hohoe (Ghana), 1996–2001.

neither windrun nor rainfall could be used directly to predict *P. truncatus* trap catch (Table 2), thus attention was focused on the statistically significant variables, humidity and temperature, to give an explanation of the occurrence and varying heights of the Harmattan and Mid-year peaks.

Humidity

During the course of a typical year, humidities varied widely from 20–80% RH (as measured at mid-day). There were very clear annual patterns with below average humidities in the period of the Harmattan in December/February and above average in May/October (Fig. 2). Across the 5 years of study, there was a sharp change in humidity conditions during the Harmattan of 1998/99 when humidities only dropped to 45%; unusually this was not associated with a decline in *P. truncatus* catch (Fig. 1). In other years, the declines varied from 38% to as low as 20%, suggesting that, in 1998/99, the humidity did not seriously limit flight activity and that another factor(s) was the dominant influence over the numbers of catches in flight traps.

Temperature

During the course of a year, mean temperatures generally rose in the period from September through to March/April. Thereafter, they declined, reaching their lowest values in the 3 months from July to September (Fig. 3). In 1996/97 and 1997/98, *P. truncatus* catches continued to rise as these mean temperatures fell and only went into decline at the time that the lowest temperatures, 25–26 °C, were reached. A similar pattern was observed in 1999, except that the very high levels of *P. truncatus* catch had already been reduced somewhat in advance of the lowest mean temperature, but there was, as before, a final substantial drop at the lowest daily mean temperatures of about 25 °C (Fig. 3).

The typical CUSUM plot for temperature during the course of a year appeared to be a bell-shaped curve (Figs 4a,b). There was no consistent pattern between rise in mean temperature and change in catch in 1996/97 (Fig. 4a) or in 1997–98. However, in 1998/99, the CUSUM slopes for temperature and *P. truncatus* catch were similar; two offset bell-shaped curves with catch lagging 4–12 weeks behind (Fig. 4b). This indicates a linear relationship between catch and mean temperature; there was a strong positive regression of temperature on catch compared with humidity

(Table 2). The CUSUM plot for humidity (Fig. 2) suggested that, during 1998/99, a factor other than humidity was controlling *P. truncatus* catch. From the evidence available, this factor appears to be temperature.

The mean temperatures used in this study were derived from the average of daily maxima and minima. A comparison with mean daily temperatures derived from hourly observations shows that means from maxima and minima always give values that are higher, by on average (\pm SE) 1.3 ± 0.22 °C. The discrepancy was least in July, with a 0.78 °C difference, and greatest in September, with a 2.0 °C difference. The difference between the months is affected by the extent to which the diurnal temperature peak is spread across the day, the more evenly it is spread, the lower the deviation between the two means. This has an important bearing on the performance of the rule-based model since this has to rely on temperature means derived from maxima and minima.

Explanation of observed pattern of *P. truncatus* flight activity at Hohoe

We suggest that RH (linked to rainfall distribution) together with temperature are major determinants of the observed patterns and magnitude of *P. truncatus* trap catches in the Hohoe area of the Volta Region. The two typical peaks in *P. truncatus* flight activity each year could arise as follows. During the short rains, from September onwards, the moist conditions and rising temperatures lead to a rise in *P. truncatus* population that starts to manifest itself as increased beetle catch from November onwards. As rainfall diminishes, moisture conditions become limiting and a sharp fall in *P. truncatus* activity is recorded. This defines the first peak. The long rains start after the Harmattan and as heavy rain set in, mean temperatures begin to fall. It would be expected that humidities raised above those of the Harmattan would favour *P. truncatus* population growth and, although temperatures fall, they remain long enough in a favourable range (29–27 °C) (Subramanyam & Hagstrum, 1991) for good *P. truncatus* population growth to occur. Together, these factors promote a rapid rise in *P. truncatus* catch. As the lowest mean temperatures are reached, there is a sharp fall in *P. truncatus* trap catch, defining the second peak. In essence, the Harmattan peak is generated by a rise in temperature and terminated by lack of moisture. The Mid-year peak is generated by wet

Table 2 Linear regression of climatic variables on *Prostephanus truncatus* trap catch at Hohoe (Ghana, Volta Region) for the period November 1996 to September 2001

Period	Variable	<i>b</i> *	<i>F</i>	<i>P</i>
November 1996 to September 2001	Mean percentage relative humidity (at mid-day)	–0.27	8.25	0.005
	Mean temperature	0.23	6.24	0.014
	Mean windrun	0.11	1.84	0.177
	Mean rainfall	0.13	1.42	0.236
November 1998 to October 1999	Mean percentage relative humidity (at mid-day)	–0.34	3.27	0.083
	Mean temperature	0.56	11.64	0.002

**b*, Standardized regression coefficient.

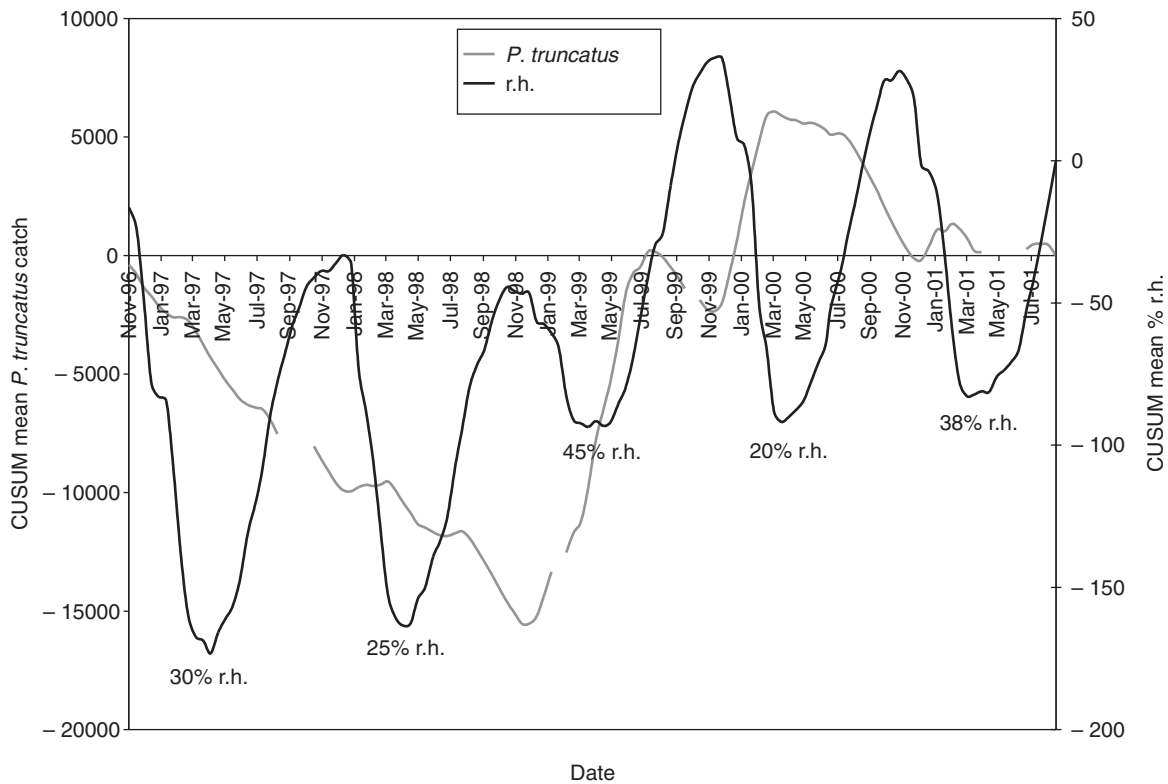


Figure 2 CUSUM for mean percentage relative humidity at Ho and *Prostephanus truncatus* catch at Hohoe (Ghana, Volta Region), 1996–2001.

conditions with falling temperatures and starts to decline at about the time when mean temperatures fall to 26 °C (more like 24–25 °C if the error in calculating daily means is taken into account).

Differences between years in climatic conditions could account for dramatic differences in the magnitude of *P. truncatus* trap catches. In Hohoe, in 1996/97 and 1997/98,

low moisture conditions terminated the Harmattan peak by March. The pattern in 1998/99 was quite different. Rainfall and humidities remained high and a single massive peak developed. The effect of favourable moisture conditions was that the CUSUM curve of *P. truncatus* catch was almost identical in shape to that for mean temperatures (Fig. 4b). This suggests that if humidities remain above a

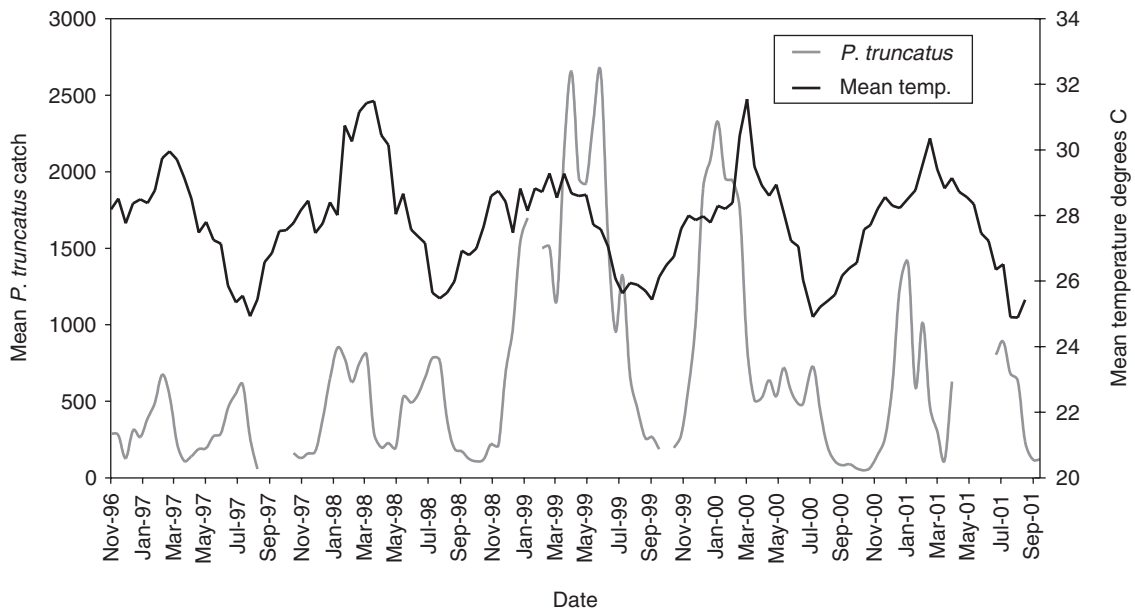


Figure 3 Mean temperatures at Ho and *Prostephanus truncatus* catch at Hohoe (Ghana, Volta Region), 1996–2000.

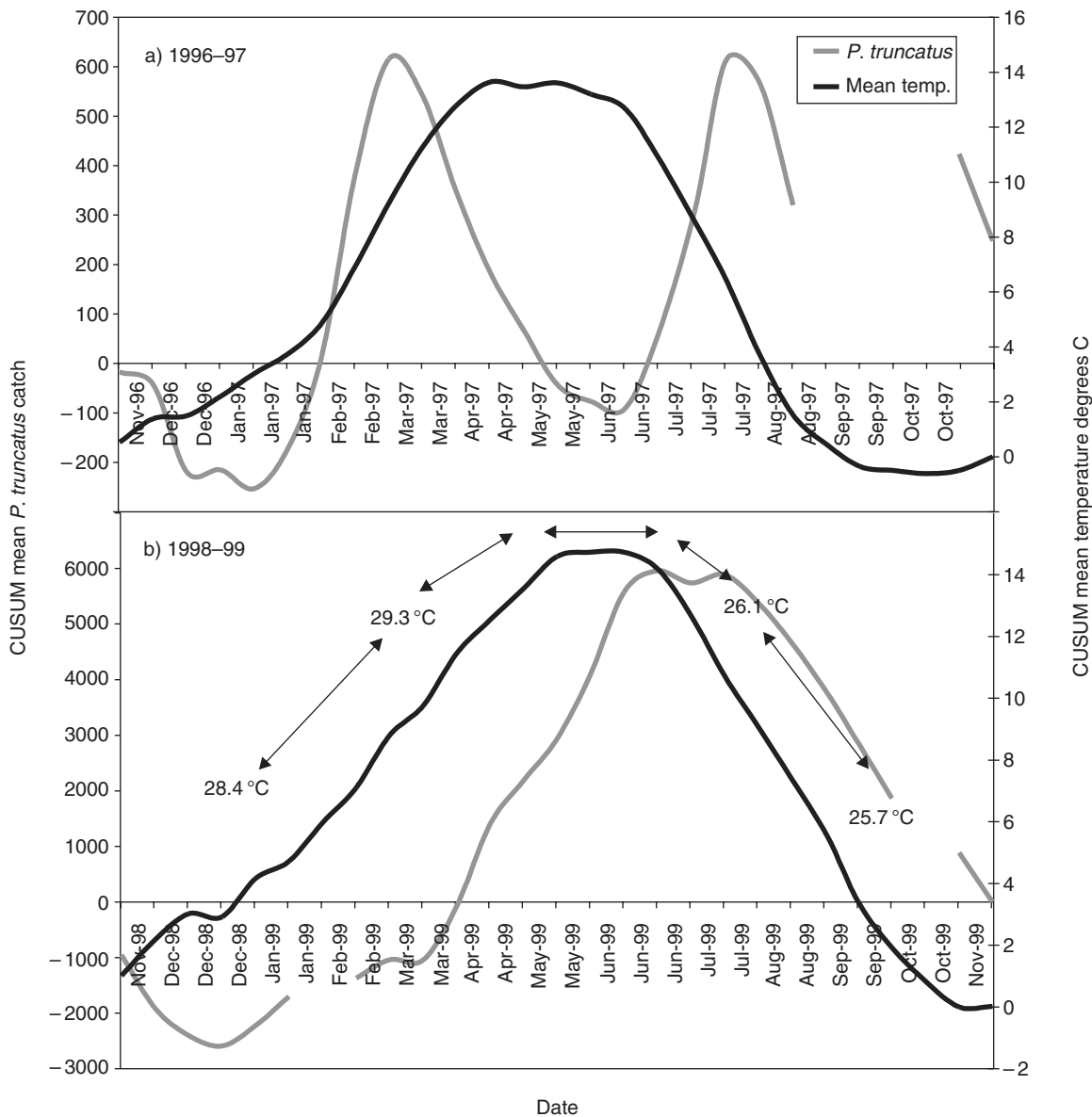


Figure 4 CUSUM mean temperature at Ho and *Prostephanus truncatus* catch at Hohoe (Ghana, Volta Region) in (a) 1996-97 and (b) 1998-99. The temperatures indicated in (b) are means illustrating changes during the course of the year.

critical value, in this case the lowest two week period averaged about 45% with the majority of days in this period above 50%, then the major determinant of *P. truncatus* catch is probably mean temperature.

In 1998/99, it seems likely that the typical two peaks merged into a single large peak because the habitat did not dry out fully during the Harmattan. Following the Harmattan, there was no need for the rains to rehydrate the food sources before the population could continue to grow. As the population was already active and at a high level, it continued to increase even further until exceptionally heavy rains in May/June followed by low temperatures in August brought sharp reductions in *P. truncatus* catch.

It is clear that temperature and humidity have a profound effect on annual and seasonal variations in the abundance

of *P. truncatus* dispersing by flight and that these factors could be used in a rule-based model to predict catches.

Rule-based climate model to predict *P. truncatus* trap catch

Six rules for predicting trap catch (Table 3) were elaborated from the foregoing observations on the responses of *P. truncatus* flight behaviour to temperature and humidity, allowing lags for long-term effects, as well as from prior knowledge and assumptions about the biology of the pest. Climate data were entered into a spreadsheet as 2-weekly means of daily mean temperature (T) and percentage RH at mid-day (R) and the actual number of days with less than 40% RH at mid-day (H).

Table 3 Varixables and parameters used for the rule-based model

Rule 1	$F = f(T, R)$	Estimation of favourability of mean temperature (T) and mean percentage relative humidity (R) for <i>Prostephanus truncatus</i> development and survival. Discrete values of r are selected from a table.
Rule 2	$r_t = \begin{cases} \frac{F_t}{F_{t-1}} & \text{if } F_t < 2.0 \\ \frac{F_t}{F_{t-1}} + 0.2F_t - 0.39 & \text{if } 2.0 \leq F_t < 2.3 \\ \frac{F_t}{F_{t-1}} + 0.1 & \text{if } F_t \geq 2.3 \end{cases}$	r_t is a change in the favourability of conditions between two-week periods and determines how much the previous estimate of the potential dispersing population should be increased or reduced. If consecutive F -values are the same then r_t will return a value of 1, leading to no change in numbers dispersing. Under favourable conditions, $F \geq 2$, some increase is expected so r_t is supplemented in increments starting at 0.01 and increasing by 0.02 for $F=2.1$ – 2.3 but by a flat rate of 0.1 when $F \geq 2.3$.
Rule 3	$r_t := 1$ if $\sum_{i=3}^{-1} H_i > 20$ and $r_t > 1$	Persistent low humidity conditions, for periods of 6 weeks or more, are especially damaging to the growth of the dispersing population. When the number of days at <40% relative humidity is more than 20 any r_t values > 1 are returned to 1.
Rule 4	$D_t = \begin{cases} r_{t-4}D_{t-1} & \text{if } T_t < 26^\circ\text{C} \\ r_{t-2}D_{t-1} & \text{if } T_t \geq 26^\circ\text{C} \end{cases}$	The current potential dispersing population, D , is estimated by multiplying the value of D in the previous 2-week period by r_t from Rule 4. To provide a lag between changed environmental conditions and the numbers of beetles that develop, the r_t used is from four weeks previously if the $T \geq 26^\circ\text{C}$ in the current 2-week period or from 8 weeks previously if $T < 26^\circ\text{C}$.
Rule 5	$D_t = \begin{cases} 2D_t & \text{if } F_t - F_{t-1} < -0.7 \\ D_t/2 & \text{if } F_t - F_{t-1} > 1.1 \end{cases}$	Sudden changes in the favourability of climatic conditions for <i>P. truncatus</i> development appear to be buffered by the beetle's sheltered microhabitat. To take account of this, if between consecutive two-week periods F rises by more than 1.1 then the potential dispersing population is halved, or if it falls by more than 0.7 then the potential dispersing population is doubled. These critical values were determined by trial and error and help to eliminate small abnormal peaks and troughs.
Rule 6	$D'_t = \begin{cases} 0.15D_t & \text{if } \min(T_{t-3}, T_{t-4}, T_{t-5}) \leq 26^\circ\text{C} \\ D_t & \text{otherwise} \end{cases}$	Low temperature conditions during the development of the beetles reduces the number taking flight (D'). If temperatures are less than 26°C at 6, 8 or 10 weeks earlier then the number of flying beetles is only 15% of its potential.

An important element of the model is an estimation of the favourability of climatic conditions, F , for *P. truncatus* development. This was derived by inverting the development period curves for various temperatures and humidities, prepared by Subramanyam & Hagstrum (1991) from the data of several authors, so that long development periods equated with low F -values (Fig. 5). The value for F at 25°C and 40–50% RH was set at 1 because the beetle population is in decline at conditions below this. The values of F for more extreme climatic conditions were attenuated to take into account the difference between means based on laboratory data from a narrow range of condition and field data where means, although appearing favourable, may represent a range wide enough to include values which are unfavourable.

The first five rules of the model were used to determine the numbers of beetles that would be available to fly, referred to as the potential dispersing population (D). The first step in estimating the current value of D is to calculate r_t , the change in conditions between two consecutive 2-week period determined by dividing the current value of F by that in the previous 2 weeks (Rule 2 in Table 3). The product of D , in the previous 2-week period, and r_t , either 4 or 8 weeks previously, depending on whether prevailing temperatures are above or below 26°C, determines the current value of D (Rule 4). These rules constitute a simple discrete model of *P. truncatus* population dynamics broadly equivalent to the population model of Meikle *et al.* (1998), but lacking any density effects. On the very first occasion that the potential dispersing population is estimated (Rule 4), there is no previous value to use in the calculation. A value was therefore determined by trial and error to obtain a good fit of the model to the data. This value affects the scaling of the y -axis of all subsequent predictions and may thus be regarded as a 'scaling factor' for the environment in question. During the preparation of the model, it became apparent that *P. truncatus* developing at lower than 26°C had a reduced propensity for taking flight. The same effect has been

observed in the closely related beetle *Rhyzopertha dominica* (Perez-Mendoza *et al.*, 1999). Rule 6 (Table 3) estimates the effects of low temperature during development on the proportion of D taking flight (D'_t). When temperatures are less than 26°C at 6, 8 or 10 weeks earlier, the potential dispersing population is reduced by 85%, so that:

$$D'_t = \begin{cases} 0.15D_t & \text{if } \min(T_{t-3}, T_{t-4}, T_{t-5}) < 26^\circ\text{C} \\ D_t & \text{otherwise} \end{cases}$$

Comparison of trap catch predicted by the model and actual catch

The actual trap catch observed and that predicted by the rule-based model match very closely (Fig. 6). The greatest deviation between modelled and actual catch occurs during December to March in years when there are sudden rises and falls in humidity, such as 1996/97, 1997/98 and 2000/01. In these years, there is consistent under estimation (Table 4). It would appear that the rules governing the outcome in this situation have still to be accurately defined. When the Harmattan is not severe, so that there is a large Harmattan peak in flight activity, the deviation is small, only +5% in 1998–99 and –1% in 1999–00 (Table 4). There is a tendency for the Mid-year peak to be over-estimated, on average by about 13%. It would appear that large year to year variations in the numbers of *P. truncatus* distributing by flight are explained by climatic variations and that in the case of Hohoe humidity and temperature are the most important factors.

The predicted potential dispersing populations (D) is considerably greater than the predicted numbers taking flight (D') in July and August when temperatures are lower (Fig. 7). When temperatures subsequently rise in September/October, this large breeding stock apparently gives rise to the very rapid increase in dispersal observed in November. The height of the Harmattan peak is thus a function of the size of the resident population of beetles during the cooler period and how favourable conditions are during the Harmattan, especially how limiting moisture

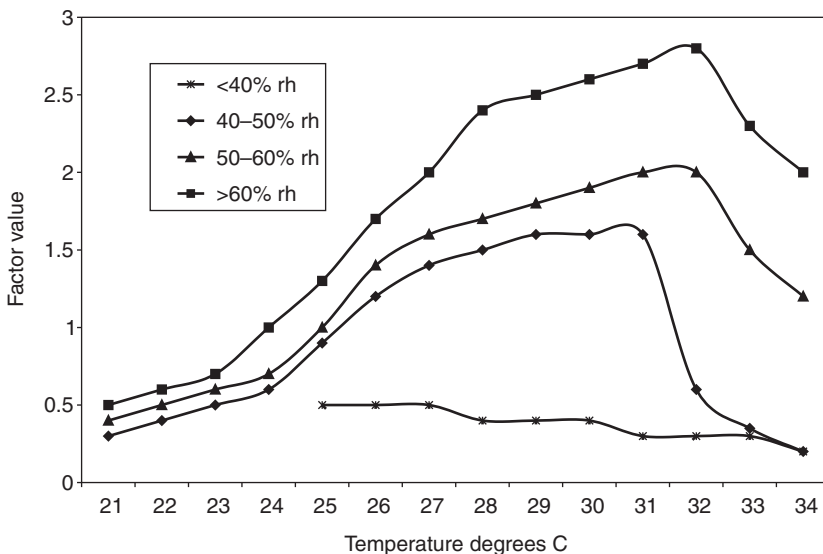


Figure 5 Factor values, associated with temperature and humidity combinations, used in the climate model for determining the potential *Prostephanus truncatus* trap catch.

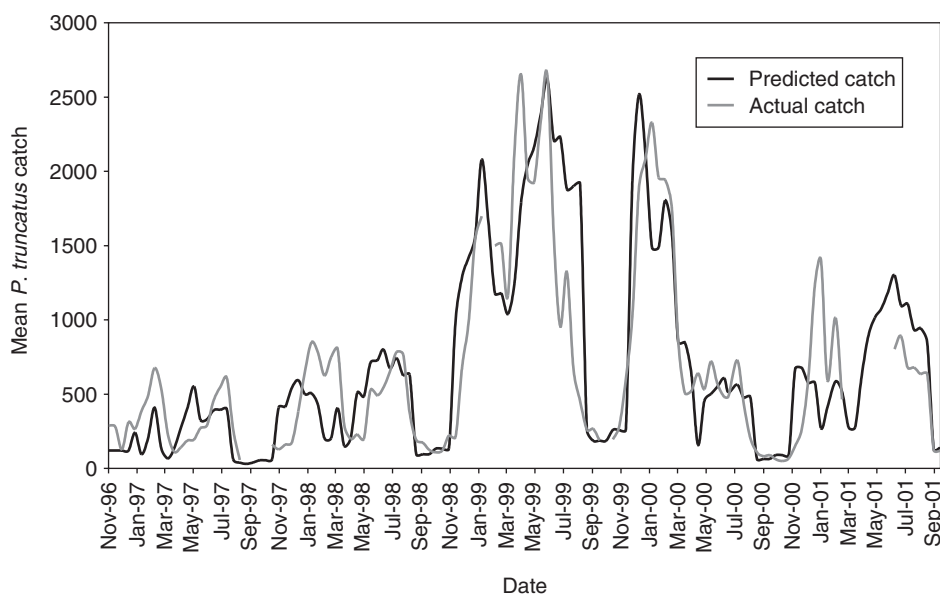


Figure 6 Actual mean *P. truncatus* trap catch at Hohoe (Ghana, Volta Region) compared to the catch predicted by the rule-based climate model, 1996–2001 ($n=20$).

conditions become. There is further very rapid increase during the hotter period of the year (March/May) in response to the rise in ambient humidity. Presumably conditions are sufficiently warm that this rise is achieved by rapid population increase from a much smaller initial population than that responsible for the Harmattan peak.

Observations at Nkwanta (Ghana) and Morogoro (Tanzania)

Nkwanta, like Hohoe, had a Harmattan and a Mid-year peak in *P. truncatus* flight activity (Fig. 8). To improve the fit of the model for Nkwanta data, two modifications to the rules were adopted. For Rule 3, which reduces r_t values due to low humidity conditions in the preceding 6-week period, r_t values greater than one are halved rather than reduced to one as in the model for Hohoe.

$$r_t = r_t/2, \sum_{i=1}^{t-3} H > 20 \text{ and } r_t > 1$$

This lessens the effect of low humidity on the trap catch since ΔF -values at the end of periods of low humidity in

Table 4 Percentage deviation of the area under the curve of *Prostephanus truncatus* trap catch predicted by the rule-based climate model from the actual trap catch in Hohoe (Ghana, Volta Region) for the two annual peaks in trap catch

Year/annual peak	Harmattan	Mid-year
1996–97	–56%	+15%
1997–98	–21%	+21%
1998–99	+5%	+18%
1999–00	–1%	–1%
2000–01	–25%	–

Nkwanta tend to be very high (e.g. in excess of 5). These are thus reduced to values over 2.5 instead of to 1. It is not certain whether this is required because of a greater tolerance of beetles to dry conditions in Nkwanta or because the host substrate is more able to retain moisture. Rule 6, the critical temperature to determine the number of beetles taking flight, was increased to 28 °C. The predicted and actual trap catches in Nkwanta are closely matched (Fig. 8).

In Morogoro, *P. truncatus* catch rose to a single large peak in the period November 1997 to September 1998. In the following 12 months, *P. truncatus* numbers remained low during the entire period of trapping (Fig. 9). Only one modification was required to improve the fit of the model for Morogoro data; the critical temperature to reduce the number of beetles taking flight (Rule 6) was increased to 28.5 °C. The predicted and actual trap catches in Morogoro are very closely matched (Fig. 9) with a large annual peak in 1997/98 and only low peaks in the other years studied.

Discussion

When *P. truncatus* abundance was observed to be exceptionally high, presenting a greater risk to farmers, there was a coincidence of favourable temperatures and humidities. At Hohoe in Ghana, this happened when the Harmattan was less severe so that moisture conditions remained high enough for the beetle to be able to benefit from the higher temperatures at that time of year. At Morogoro in Tanzania, there was an exceptionally high peak in numbers in 1998. Although not presented here, a check of the climate data for 1998 shows that the normal rise in temperatures in November/December unusually coincided with a rise in humidity; in other years, humidities only rose once temperatures had already started to decline. Farmers observed during 1998 that they were suffering unusually heavy attack by

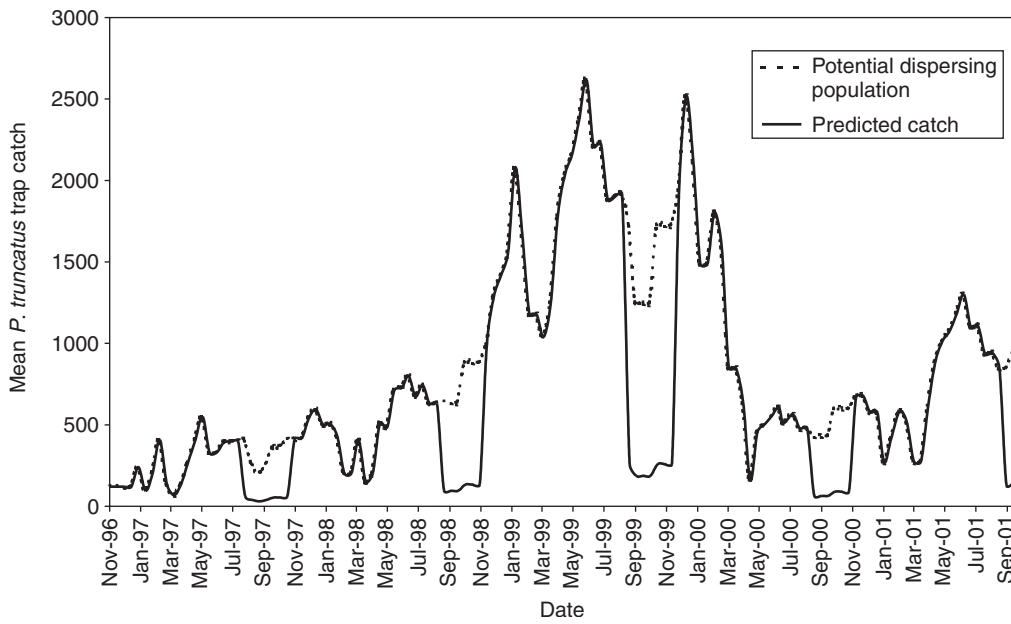


Figure 7 The potential and predicted numbers of flying *Prostephanus truncatus* at Hohoe (Ghana, Volta Region).

P. truncatus in their maize stores (William Riwa, personal communication). This corroborates both the abnormally high peak in dispersing beetles and the connection between this and the increased likelihood of stores becoming infested. In Hohoe, the years of high pest flight activity coincided with poor harvests where storage periods were short; consequently, farmers were largely unaffected (S. Addo, unpublished data).

In Ghana, the towns of Hohoe and Nkwanta typically had distinct Harmattan and Mid-year peaks in *P. truncatus* flight activity. Similar peaks in catch have been reported previously from Mono province in Benin (Borgemeister *et al.*, 1997b) but not from the coastal zone where there is a single annual rise and fall, presumably because humidities there do not drop below 50% during the period of the Harmattan. In the case of the Benin coastal zone, *P. truncatus* trap catch

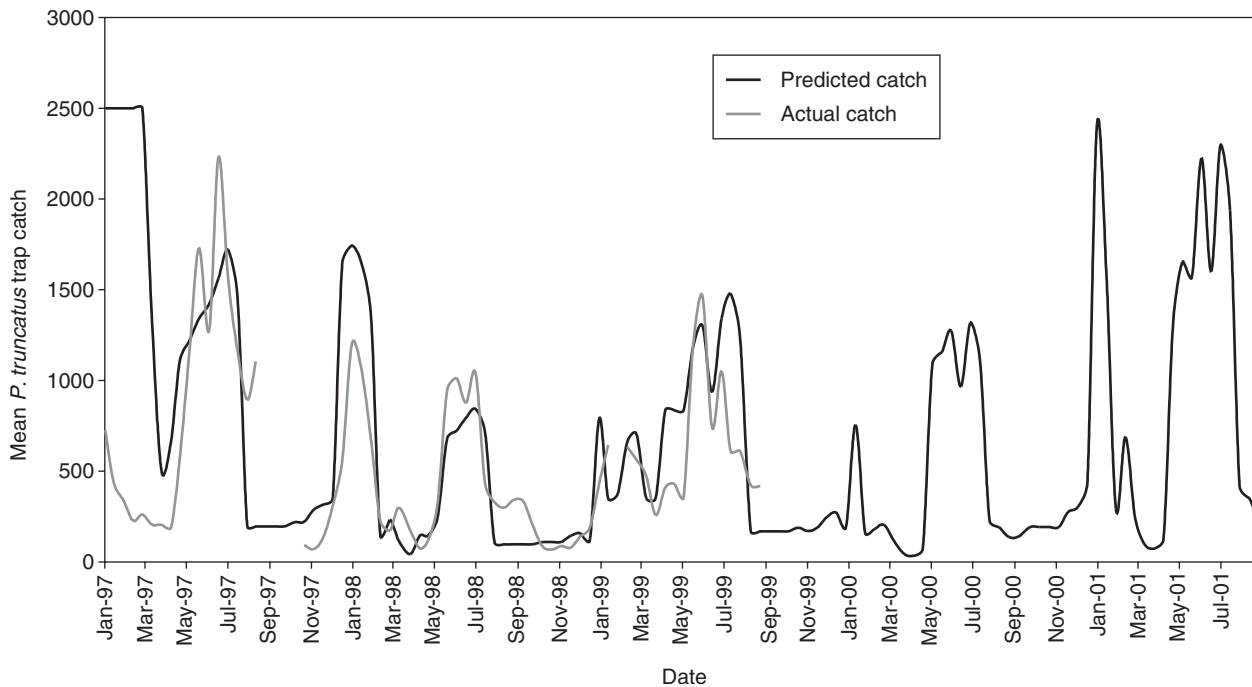


Figure 8 Actual mean *P. truncatus* trap catch in Nkwanta (Ghana, Volta Region) compared to the catch predicted by the rule-based climate model, 1997–99 ($n = 20$).

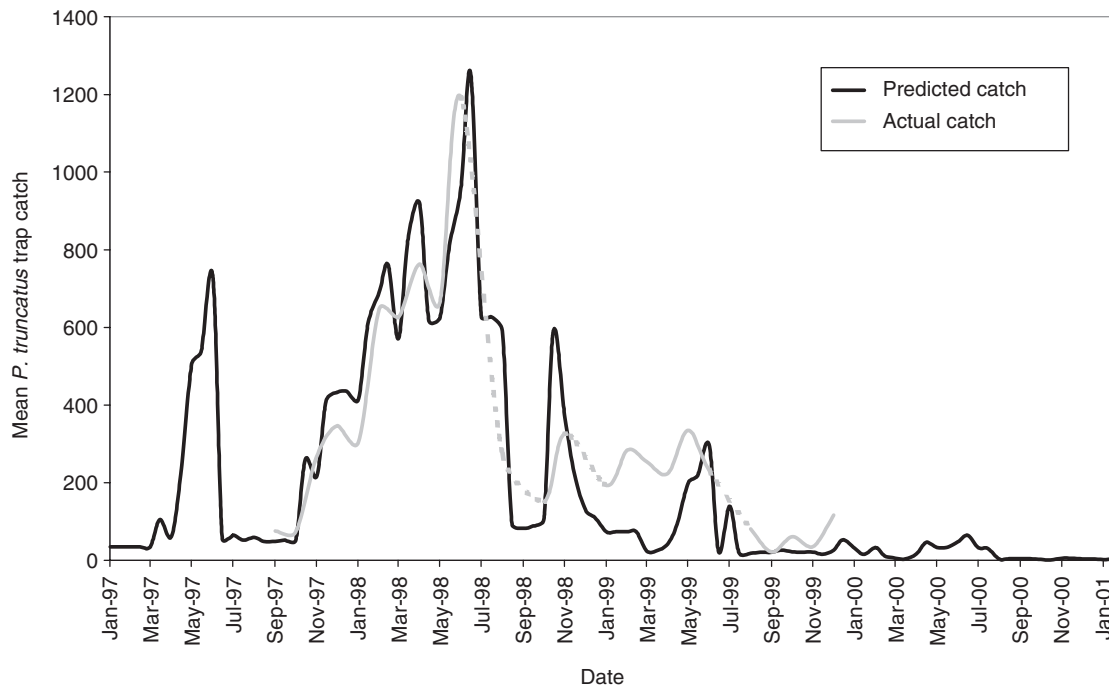


Figure 9 Actual mean *Prostephanus truncatus* trap catch in Morogoro (Tanzania) compared to the catch predicted by the rule-based model (dotted line shows interpolated values for actual catch) ($n=9$).

was related only to mean temperature (Borgemeister *et al.*, 1997b; Scholz *et al.*, 1998), a finding consistent with the current study in years when humidity is not limiting. The observed response of the beetle to low humidity conditions confirms previous reports. On wood, which is believed to be the common host in the natural environment, it has been concluded that *P. truncatus* cannot breed unless the moisture content is above 10% (Nang'ayo *et al.*, 1993). For a variety of tree species, held at 55% RH, the equilibrium moisture contents ranged from 9.5–10.4% (Nang'ayo, 1996). Thus, humidities much below 50% are unlikely to be able to support *P. truncatus* development on the wood species that have been tested. However, the moisture content/RH equilibrium seems to be a little different for maize. At 40% RH, the moisture content of grain of a local Tanzanian variety is still 10.5% and the intrinsic rate of increase of *P. truncatus* is 0.46/week compared with 0.73/week at 70% RH, equivalent to 14.2% grain moisture content (Hodges & Meik, 1984). Thus, *P. truncatus* can probably develop on maize, and possibly some other hosts, under rather drier conditions than on the wood species that have been studied.

An interesting feature of the model is the apparently strong effect of low temperatures during development on the beetle's subsequent tendency to distribute by flight (Rule 6). The critical temperatures used in Rule 6 varied between habitats, Hohoe 26°C, Nkwanta 28°C and Morogoro 28.5°C. Nkwanta and Morogoro are savannah woodland/short grassland habitats which would be expected to have more steeply rising and falling daytime temperatures than Hohoe which is in the tropical rain forest–savannah transition zone. They would thus show

greater positive deviation in the calculation of the daily mean from the daily maximum and minimum temperature and this probably accounts for the higher critical values. Even Hohoe has a positive deviation ranging from 0.7°C to 2.0°C. This suggests that the true critical temperature is between 24.0° and 25.3°C. It is not certain why low temperatures can have such long-term influences. Low temperatures would be expected to result in a slowing of development, and hence slower recruitment to the habitat, but the model suggests continued development with a lower proportion of those beetles that would potentially take flight actually doing so. This happens despite the subsequent exposure of these beetles to more favourable ambient temperatures in September/October. It is possible that low temperatures affect food supply so that fewer beetles are in a suitable nutritional state to undertake energy consuming activities like flight. In the case of the related bostrichid *Rhyzopertha dominica*, beetles collected in the U.S.A. in summer had a higher lipid content and greater tendency to fly than beetles collected in spring or autumn (Perez-Mendoza *et al.*, 1999). In the case of *P. truncatus*, it would be easy to devise experiments to test whether the temperature at which beetles develop has a direct effect on propensity for flight but more difficult to include the influences of environmental conditions on the nutritional status of the pest.

In the model of Nansen *et al.* (2001), day length is an important variable for predicting *P. truncatus* flight activity. There is a suggestion that photoperiod may affect the flight activity of *R. dominica* (Aslam *et al.*, 1994). However, the evidence is equivocal as the two extremes tested, 6 hours and 18 hours light, differed significantly in flight activity for a

laboratory strain but not for a field strain of the beetle. Nansen's model was able to predict trap catch data from sites 6°N to 9°N, although it missed a very distinctive Mid-year peak in 1998 and consistently under-predicted catch in 1999. In addition, it did not work at 10°N where conditions tend to be hotter and drier. It was suggested that it might not be driven by the same environmental conditions in all agro-ecological zones; the rule-based model also showed less accurate predictions when presented with more severe conditions. A model based on day length would also not work close to or on the equator' as Dingle (1972) has noted, those insects '...whose range spans the equator, where photoperiods are essentially constant, must rely directly on ultimate environmental factors'. Day length was not included in the rule-based model and it does not appear to be deficient because of this. Day length may be a proxy for the long-term effect of temperature on propensity for flight and/or other factors such as the favourability of plant hosts.

It is clear that for those habitats studied, the rule-based model offers a convenient and easily affordable means by which extension services could predict years of greater *P. truncatus* flight activity. Once predictions of beetle numbers have been made and they exceed a threshold, based on the known probabilities of store infestation at different frequencies of dispersing beetles (Birkinshaw *et al.*, 2002), farmers can be warned to take action. In this system, the pest management threshold indicates the likelihood that a store had been attacked by a single beetle; it would thus be several months before serious damage would be expected. This gives a reasonable lead-time for pest management action such as marketing early or investment in methods to kill the pest such as pesticide treatment. Predictions of flight activity were consistently under estimates when climate was more severe. However, this inaccuracy would seem unlikely to affect pest management decision making because, under these conditions, catches were in any case low and so would be very unlikely to trigger any specific advice to farmers. Conversely, when conditions were favourable for the pest, the predictions were more accurate, although they tended to be overestimates. Thus advise to farmers would be expected to be 'safe' (i.e. they are more likely to be advised to take action when it is not needed than advised not to take action when it is needed).

There are other possible uses for the model. In advance of the arrival of the pest in a particular country or province, the model could help to predict the likelihood that it will cause significant problems. However, any such predictions would have to be treated with caution because, although the model works well under a range of conditions in which *P. truncatus* is likely to be a significant pest, it has yet to be tested under more extreme conditions. For example, Nansen *et al.* (2001) found their model would not work in northern Benin (10°N). Another difficulty comes in setting the scale for the catches in situations where there are no previous data on *P. truncatus* trap catch. The scale confounds aspects of habitat suitability such as hosts, predators and parasites and, in the absence of any trap catch data, can only be set to what would be expected in other similar environments for which there are data. Earlier predictions

on the potential of *P. truncatus*, based on laboratory observations on development on maize under a range of temperatures and humidities, suggested that it would develop best in warm moist conditions (Haubruge & Gaspar, 1990). In contrast, field observations across five regions of Mexico, suggested that there is higher abundance in cooler, more temperate areas, a relationship evident even from the raw data (Tigar *et al.*, 1994). This discrepancy warns that habitat suitability is more complex than just measures of temperature and humidity. Nevertheless, the current study shows that in habitats that have a seasonal climate with distinct dry periods, *P. truncatus* develop best under warm moist conditions. Permanently warm moist conditions may be unfavourable because potential hosts may not dry out sufficiently, or seasonal die back on trees which, as suggested by Nang'ayo *et al.* (1993), provides suitable niches for the pest, may not occur.

Another use for the model might be to obtain some measure of the impact of a predator of *P. truncatus*, *Tere-trius nigrescens* (Lewis). This histereid beetle has been introduced from Central America into several African countries. Determining the impact of this predator has been problematic, not least because its effects on *P. truncatus* have not been separable from those of climate. If suitable data are available from before the establishment of the predator in a particular locality then, after predator introduction, the magnitude of any fall in actual trap catches below predicted catches would suggest a measure of impact on *P. truncatus*.

Acknowledgements

In Ghana, Israel Tetty, Hilarious Penne, Emmanuel Afori and Victor Afetorgbor collected and counted the pheromone trap catches and, in Tanzania, trapping data was kindly made available by William Riwa of the Plant Protection Division and the GTZ Post Harvest Project. Special thanks is due to Bruno Tran who gave invaluable help and advice in setting up the model on a spreadsheet and Richard Jones who advised on CUSUM analysis. Help and advice on the manuscript was given generously by John Holt, Niels Holst, Christian Nansen and Julia Compton. Mr P.K. Obeng of the Ho Meteorological Station kindly provided us with climate data, as did the Meteorological Station at Kilosa in Tanzania. This publication is an output from a research project funded by the United Kingdom Department for International Development (DFID) for the benefit of developing countries. The views expressed are not necessarily those of DFID. R7486, Crop Post Harvest Research Programme.

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Accepted 2 November 2002