POPULATION ECOLOGY

Sensitivity of *Prostephanus truncatus* (Coleoptera: Bostrichidae) Flight Activity to Environmental Variables in Benin, West Africa

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ABSTRACT Based on pheromone trap catches, a model of weekly *Prostephanus truncatus* (Horn) flight activity was generated for southern Benin. Using response surface regression, the following environmental variables were examined: number of rainy days per week, precipitation, minimum and maximum temperatures, minimum relative air humidity, and daylength. A time-variable, year, was included to account for the variance between years. From step-wise exclusion of variables with the lowest contribution to the model fit, a model was generated which included three environmental variables (daylength, minimum relative air humidity, and minimum temperature) that explained 55% of the total variance, and the yearly variable explaining 8%. The response surface regression analysis of *P. truncatus* flight activity revealed the following: (1) it was positively correlated with daylength when daily minimum temperature and relative air humidity were low, (2) it was positively associated with minimum relative air humidity when lower than 75%, (3) it was negatively associated with minimum temperature, (4) unexplained yearly variation was important for the predictive strength of the model, (5) interactions of environmental variables contributed substantially to the model fit, and (6) precipitation, both as mm rain and as number of rainy days, had little influence on *P. truncatus* flight activity. Independent data showed that the model predicted *P. truncatus* flight activity well elsewhere in southern Benin, whereas in central Benin new coefficients for the same environmental variables were needed to produce an adequate prediction. The model did not fit pheromone baited trap catches from northern Benin.

KEY WORDS *Prostephanus truncatus*, Benin, environmental variables, flight activity, modeling, pheromone trapping

THE LARGER GRAIN borer, *Prostephanus truncatus* (Horn), is considered native to meso America (Hodges 1994), where its original host plants are found in forest environments (Fisher 1950). *P. truncatus* was already known as a pest on stored maize by Mayan people on the Yucatan peninsula several centuries ago (Holst et al. 1999), but its appearance on the African continent was documented for the first time in the following countries: 1981 in Tanzania (Dunstan and Magazini 1981), 1983 in Kenya (Kega and Warui 1983), 1984 in Burundi (Gilman 1984), Togo (Harnisch and Krall 1984), and Benin (Anonymous 1986), 1987 in Guinea Conakry (Kalivogui and Mück 1991), 1989 in Ghana (Dick et al. 1989), 1991 in Burkina Faso (Bosque-Perez et al. 1991), 1991 in Malawi (Hodges et al. 1996), 1992 in Nigeria (Pike et al. 1992), 1993 in Rwanda (Bonzi and Ntambabazi 1993), 1993 in Zambia (Malombo et al. 1997), 1996 in Niger (Adda et al. 1996). In addition, Hodges (1994) mentioned unconfirmed reports of its establishment in Cameroon, Democratic Republic of Congo, and Guinea Bissau, Riwa (1998) referred to occurrence of *P. truncatus* in Uganda and Bell et al. (1998) to its occurrence in Namibia. In most of these countries, the documentation of *P. truncatus* incidence was based on an initial survey using pheromone traps in addition to inspections of maize and cassava stores. Pheromone trapping has also been used to document the establishment of *P. truncatus* in forest and savanna habitats in meso America (Rees et al. 1990, Tigar et al. 1993, Ramírez-Martínez et al. 1994), in East Africa (Nang'ayo 1996), and in West Africa (Borgemeister et al. 1998, Nansen et al. 1999).

Pheromone trapping is an important tool for monitoring the spread of *P. truncatus* into new areas and in studies of its general ecology. The magnitude of pheromone trap catches, however, is difficult to interpret without precise knowledge about the relation between catch, environment, and local population density. In Kenya, Nang'ayo (1996) used multiple-regression analysis to examine the effect of weather variables on biweekly pheromone trap catches from 1991 to 1995 and concluded that mean daily temperature and relative air humidity explained 7% of the total variance. Similarly, Borgemeister et al. (1997b) used multiple-regression analysis to examine the effect of climate variables and a time-variable on weekly pheromone trap catches from April 1992 to December 1995 in southern Benin. They found that 30% of the

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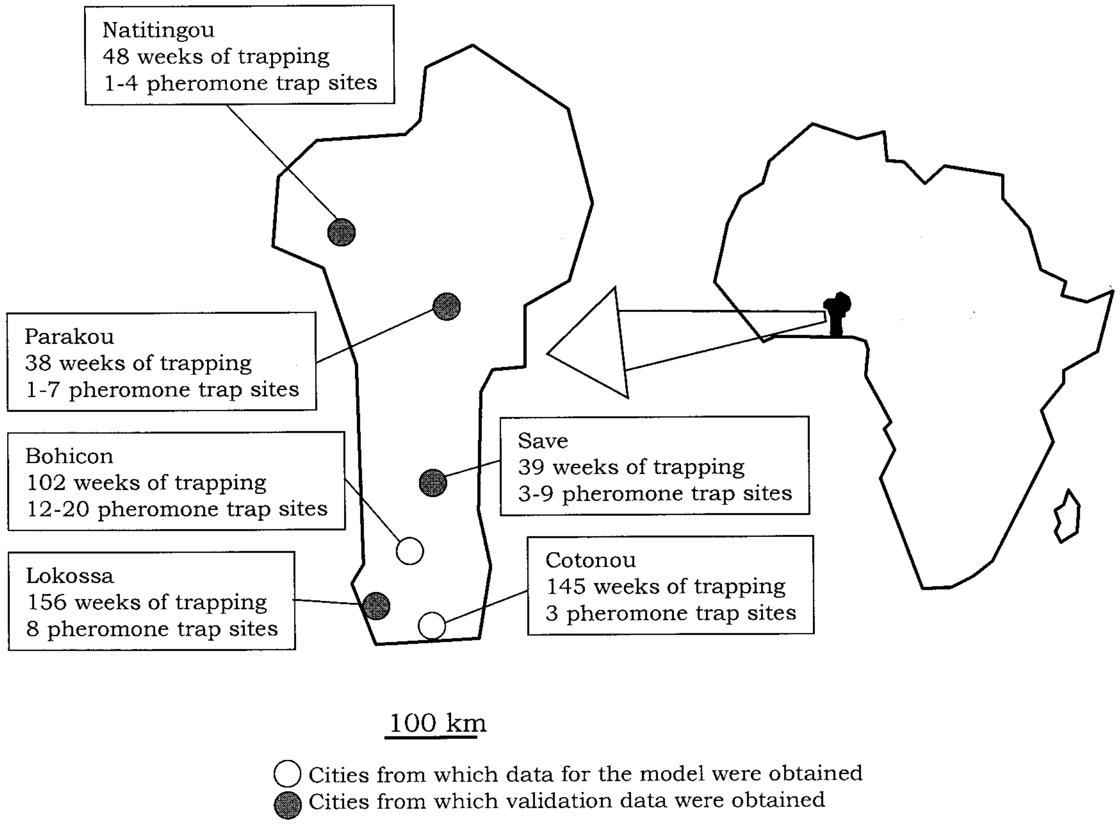

Fig. 1. Pheromone trap catches from sites <20 km from Cotonou and Bohicon (white circles) in southern Benin, West Africa, were used to develop the model of *P. truncatus* flight activity. Climate data used for the surface regression analysis of trap catches were obtained from the meteorological station in both cities. Pheromone trap catches from sites <20 km from four cities (gray circles) were used for validation of the flight activity model. Mean trap catches from 1997 to 1999 from eight sites near Lokossa were used. Climate data for Lokossa were interpolated assuming linear north-south changes between Cotonou and Bohicon. Validation data were also obtained from Save, Parakou, and Natitingou.

total variance was explained by the "year of trapping" and 10% by mean daily temperature. Neither of these studies included the effect of interactions among variables, and the regression models were not validated with other time series or with data from other locations.

In this article we conduct a response surface regression analysis to determine to what extent pheromone trap catches of *P. truncatus* can be explained by spatiotemporal variation in environmental conditions. The regression model was derived from data from southern Benin and was successfully validated against an independent data set from the same region. Validation against data from central and northern Benin was, however, less successful.

Materials and Methods

Pheromone Trap Catch Data. Although the relationship between pheromone trap catches and *P. truncatus* flight activity is not known in detail, pheromone trap catches during an extended time period were here assumed to be a direct indicator of *P. truncatus* flight activity. Weekly pheromone trap catches and weather data near Cotonou (6° 21 min N, 2° 26 min E) and Bohicon (7° 20 min N, 2° 8 min E) in southern Benin (Fig. 1) were used to generate a model of *P. truncatus* flight activity. At each location the following number of pheromone traps was operated and used to calculate weekly averages: Cotonou: Three pheromone traps, placed on the International Institute of Tropical Agriculture (IITA) station, 15 km north of Cotonou, for 145 wk 1997–1999. Bohicon: From February 1998 to September 1998 catches were obtained from 12 pheromone traps, and from September 1998 and throughout 1999 pheromone trap catches were obtained from an additional eight pheromone traps. In total, 102 wk of pheromone trapping were analyzed from this location.

Delta-type sticky traps (Pherocon II, Trécé, Salinas, CA) and *P. truncatus* lures containing 1 mg T1 and 1 mg T2 (Agrisense-BCS, Pontypridd, UK) were used, and all pheromone traps were placed in well-exposed locations. Both pheromone traps and lures were changed weekly. Most of the pheromone trap sites were located in farming areas, but the mean phero-

Table 1. Minimum, maximum, and mean environmental conditions in Cotonou (145 wk) and Bohicon (102 wk) in southern Benin in 1997–1999

	Min temp, °C	Day length (dec. hour)	Min. humidity, %	Max. temp, °C	Precipitation (mm)	Rainy days (prop.)
Min	19.73	11.66	9.57	26.12	0.00	0.00
Max	28.76	12.58	83.57	39.71	32.81	1.00
Mean	24.19	12.13	60.34	32.02	3.97	0.26
SD	1.539	0.268	15.09	2.8	5.798	0.25
Mean − 2 SD	21.12	11.59	30.15			
Mean − SD	22.65	11.86	45.25			
Mean	24.19	12.13	60.34			
Mean + 2 SD	25.73	12.40	75.43			
Mean + SD	27.27	12.66	90.52			

Day length is in decimal hours, precipitation (mm) is total per week, and rainy days is the proportion of days with rain per week. Values 1–5 represent the mean ± 1 and 2 standard deviations for each variable included in the model. These values were used in the presentation of *P. truncatus* flight activity model response to each of the variables (Figs. 3–5).

mone trap catches from Bohicon included data from 16 pheromone trap sites in the Lama forest reserve ≈20 km south of Bohicon and from four pheromone trap sites in farming areas just outside the forest.

Analysis. A model of *P. truncatus* flight activity would only be valid if flight activity on adjacent sites were following the same seasonal pattern in response to the environment, independently of whether the flight activity at a given site is high or low. Two of the pheromone traps near Bohicon were selected to test this. The pheromone traps were located less than 5 km apart, were placed at the same height above the ground (1.5 m), and were changed weekly on the same days in 1998 and 99. Trap 1 was placed inside the Lama and trap 2 was placed in a maize growing area on the northeastern side of the forest.

The main purpose was to develop a robust flight activity model based on a small number of standard environmental variables, which are easily obtainable on Internet or from weather stations. Thus, weekly means of the following six variables were included: maximum air temperature (°C), minimum air temperature (°C), minimum relative air humidity (%), precipitation (mm), number of rainy days per trapping week (proportion), and daylength (decimal hours). Climate data were obtained from the meteorological stations of ASECNA (Agence pour la SECurité de la Navigation Aérienne en Afrique) in Cotonou and Bohicon. Daylength was obtained from http://riemann.usno.navy.mil/AA/data/docs/RS OneD. A discrete yearly time-variable with values 97, 98, and 99 was included to account for systematic differences between the three years.

The Response Surface Regression Procedure (PROC RSREG) in SAS/STAT (SAS Institute 1989) was used to analyze the relationship between environmental variables and *P. truncatus* flight activity. This type of regression examines linear and quadratic responses of variables separately, to determine whether the dependent variable response is mainly linear or quadratic. It also includes the effect of pairwise linear interactions among variables. Further details on the use of this regression procedure are available in Freund and Littell (1991). With seven environmental variables in the full model of *P. truncatus* flight activity, 36 parameters are included: seven linear responses, seven quadratic responses, 21 linear interactions, and the intercept. Thus, the first step was to reduce the number of parameters by excluding environmental variables with the lowest contribution to the model fit. The total contribution (both linear and quadratic responses and in linear combination with other variables) of each of the environmental variables is calculated by the RSREG procedure in SAS, and in single steps, the environmental variable with the lowest contribution to the model fit (lowest *F* value) was excluded.

Because both linear and quadratic responses and linear interactions are included in the model, the coefficients are difficult to interpret, and the flight activity response is not easily visualized. It was therefore decided to choose five values for each variable included in the model and present the flight activity response when two of the variables were held constant at each of the five levels. The five values of each variable were equal to the mean ± one and two standard deviations (Table 1).

Validation. As part of the on-going monitoring of *P. truncatus* incidence in West Africa, workers at IITA have maintained pheromone traps at eight sites near Lokossa (6° 39 min N, 1° 51 min E) in south western Benin since 1991 (Fig. 1); the sites were described by Borgemeister et al. (1997a). This region is one of the main maize-producing regions in Benin and was also the area of Benin where *P. truncatus* was first recorded (Anonymous 1986). Three years of weekly pheromone trapping data (total of 156 wk from 1997 to 1999) were used for validation of the regression model. Climate data for Lokossa were interpolated, based on weighted geographical distance from the weather stations in Cotonou (two-thirds) and Bohicon (one-third) assuming that climate changes linearly in south-north direction. The model was also evaluated against three data sets from central and northern Benin (Fig. 1): 39 weekly pheromone trap catches from January 1997 to March 1998, from three to nine trap sites in a 20-km range from Save (8° 2 min N, 2° 29 min E); 38 wk of pheromone trap catches from February 1996 to June 1998 (weekly pheromone trapping was conducted approximately every third week), from one to

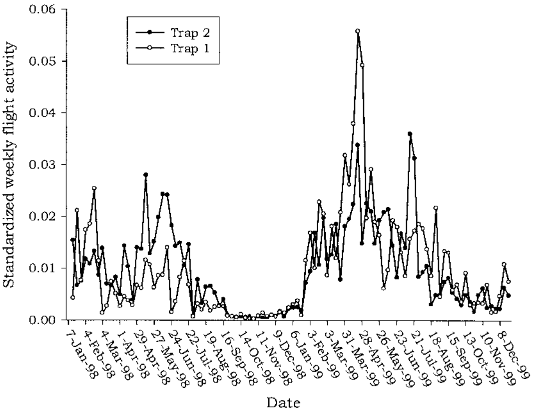

Fig. 2. Spatial variation in weekly *P. truncatus* flight activity. Standardized (dividing each weekly trap catch with the total for the 102 wk) weekly *P. truncatus* flight activity in 1998 and 1999 at two trap sites <5 km apart inside (trap 1) and just outside the Lama forest (trap 2) ≈18 km south of Bohicon (Fig. 1). For the 102-wk pheromone trapping period, trap 2 caught 45,450 *P. truncatus* individuals, while trap 1 caught 16,700.

seven trap sites in a 20-km range from Parakou (9° 20 min N, 2° 38 min E); 48 wk from February 1996 to June 1998 (weekly pheromone trapping was conducted approximately every third week), from one to four pheromone trap sites <25 km from Natitingou (10° 18 min N, 1° 22 min E). Climate data for validation sites were obtained from the meteorological stations in all three cities. Pheromone lures and sticky traps in validation data sets were the same as the ones used at the pheromone trap sites in Cotonou and Bohicon.

Results

Spatial Variation of Pheromone Trap Catches. Of the two Bohicon pheromone traps selected to test the similarity of trap catch patterns in nearby traps, trap 1 caught 16,700 *P. truncatus* individuals and trap 2 caught 45,450 *P. truncatus* individuals (total 1998–99) (Fig. 2). Despite the 2.7-fold difference in magnitude of total pheromone trap catches, the standardized seasonal flight activity patterns (dividing each of the weekly catches with the total for each trap) at the two sites were fairly similar with highest flight activity occurring in 1998 compared with 1999, and lowest yearly flight activity occurring from September to December. In 1998, the flight activity pattern was slightly bimodal for both pheromone traps, while the flight activity pattern in 1999 was characterized by a single peak with its maximum in late April. A linear regression analysis of standardized pheromone trap catches from traps 1 and 2 showed a significant positive correlation ($a = 0.744$, $Y_0 = 0.003$, adj $R^2 = 0.353$, $F = 56.312$, df $= 102$, $P < 0.0001$). Thus, although local conditions on trap sites caused a difference in the magnitude of pheromone trap catches, this example suggests that variables affecting flight activity on a regional level, such as climate, are responsible for the seasonal flight activity pattern.

Fit of Environmental Variables to Flight Activity. When all seven environmental variables were included in the model, 68% of the total variance in *P. truncatus* flight activity was explained (Table 2). Excluding the two nonsignificant variables (precipitation, rainy days) and the least significant of the others (maximum temperature), the explained variance only decreased to 63%. We selected this model as the best, because it explained the most variance with the fewest variables. Of the total variance explained by the model (63%), the PROC RSREG in SAS calculates the relative contribution of each of the four variables (in parentheses): daylength (27%), minimum relative air humidity (21%), year (8%), and minimum temperature (7%) (Table 3). Three of the six linear interactions, those involving minimum temperature, contributed significantly to the model fit. The response of *P. truncatus* flight activity to climate was linear, because the only significant quadratic response was year, which means that there was no clear upward or downward trend through the years. Within the examined range of environmental conditions, there was a strong positive correlation between *P. truncatus* flight activity and daylength, when minimum relative air humidity and minimum temperature were low (Fig. 3). The y-axis in Fig. 3 suggests that a 1.1-h decrease in day-

Table 2. Step-wise exclusion of the least significant variable (lowest *F*-value) in the response surface regression analysis of *P. truncatus* flight activity in southern Benin

Variable	Single-step exclusion of variables						
	Full	1 excl	2 excl	3 excl[a]	4 excl	5 excl	6 excl
Day length	23.18*	27.82*	39.33*	46.19*	43.89*	43.6*	16.43*
Min. rel. air humidity	7.12*	8.35*	9.06*	36.41*	33.65*	41.76*	
Year	10.24*	11.26*	14.87*	14.68*	14.08*		
Min temp	6.97*	8.44*	10.42*	12.45*			
Max temp	3.12*	3.38*	3.81*				
Rainy days	0.75	1.11					
Precipitation	0.72						
Adj. R^2	0.68	0.68	0.66	0.63	0.53	0.42	0.12

For each of the seven regression models tested, *F*-values show the significance of each variable included, taking into account linear and quadratic terms and linear combinations with other environmental variables. Adjusted R^2 shows the predictive strength of the regression for each combination of environmental variables. $*P < 0.0001$.

[a] Combination of variables chosen for the model.

Table 3. Results from the model of climate variables to *P. truncatus* flight activity in southern Benin

Regression	Regression analysis			P
	df	Adj. R^2	F-value	
Linear	4	0.336	52.75	<0.0001
Quadratic	4	0.1201	18.86	<0.0001
Cross product	6	0.1745	18.26	<0.0001
Total model	14	0.6306	28.29	<0.0001
	Parameters included in the model			
	df	Coefficient	t-value	P
Intercept	1	419298	2.91	0.0039
Linear response				
Min. Temperature (T)	1	4455.2	5.51	<0.0001
Year (Y)	1	−9328.4	−3.44	0.0007
Min. Rel. Air Hum. (H)	1	215.6	2.21	0.0279
Day length (D)	1	−4375.6	−0.86	0.3915
Quadratic response				
Year	1	47.8	3.50	0.0006
Min. Rel. Air Hum.	1	0.0	−1.21	0.2268
Min. Temperature	1	2.3	1.07	0.2851
Day Length	1	62.2	0.43	0.6675
Interactions				
D × T	1	−132.0	−5.46	<0.0001
T × Y	1	−31.2	−4.31	<0.0001
H × T	1	1.7	4.00	<0.0001
H × D	1	−8.1	−2.43	0.0159
D × Y	1	70.6	1.82	0.0706
H × Y	1	−1.6	−1.73	0.0855

First section shows the significance of linear and quadratic responses, and linear interactions for the response surface regression of four climate variables: day length, minimum relative air humidity, year, and minimum temperature. Second section shows the coefficients for the linear and quadratic responses of each of the four environmental variables and their linear interactions.

length would cause more than a six-fold decrease in *P. truncatus* flight activity. However, daylength had considerably less effect on *P. truncatus* flight activity when minimum relative air humidity and minimum temperature were high. *P. truncatus* flight activity was positively correlated with minimum relative air humidity, but the shape of the response surface suggests that flight activity decreases when minimum relative air humidity exceeds 75% (Fig. 4). *P. truncatus* flight activity was negatively correlated with minimum temperature, especially when daylength and minimum relative air humidity were high (Fig. 5).

Validation of the Model. The prediction of *P. truncatus* flight activity in the Lokossa region showed a seasonal pattern similar to that observed (Fig. 6), and a linear regression analysis of observed and predicted pheromone trap catches was significant (adj $R^2 = 0.448$, $F = 126.9$, df = 155, $P < 0.001$). The model validation of more northern locations was negative, because the model was not able to predict the observed flight activity at either of the three locations: Save (adj $R^2 = 0.002$, $F = 0.934$, df = 38, $P = 0.341$), Parakou (adj $R^2 = 0.028$, $F = 0.022$, df = 37, $P = 0.881$), and Natitingou (adj $R^2 = 0.025$, $F = 0.023$, df = 47, $P = 0.861$). Thus, the model was only valid within southern Benin. However, fitting the four variables to *P. truncatus* flight activity at each of the validation sites showed that the same type of regression model with a site-specific set of coefficients could be used to explain flight activity in Save (adj $R^2 = 0.83$, $F = 9.2$, $P < 0.0001$) and Parakou (adj $R^2 = 0.783$, $F = 5.7$, $P < 0.0001$), but not in Natitingou (adj $R^2 = 0.281$, $F = 0.938$, $P < 0.543$).

Discussion

Interpretation of pheromone trap catches of bostrichids is complicated because many factors are known to affect the effective range of pheromone traps, including trap type (Key et al. 1994, Hodges et al. 1998) wind speed and direction (Boeye et al. 1994), trap height (Cogburn et al. 1984, Key et al. 1994), and weather conditions (Tigar et al. 1993, Dowdy 1994). In addition, there is evidence that pheromone traps may be selective on at least two levels by mainly attracting certain parts of the total population. Firstly, Borgemeister et al. (1998) and Scholz et al. (1997) in southern Benin, Nang'ayo (1996) in Kenya, and Birkinshaw (1998) in south eastern Ghana found that 60–75% of the *P. truncatus* individuals caught in pheromone traps were females. The pheromone lures used in these studies were the same as those used in the current study. It is not known whether females are more abundant than males in natural populations, but the sex ratio in laboratory cultures was found to be one: one by Shires (1979) and Vowotor et al. (1997). It is therefore most likely our pheromone trap catches were dominated by females as well. Secondly, Scholz (1997) showed under experimental conditions that males are more reluctant to fly than females and that young mated females are the most active flyers. Fadamiro (1996) found that young *P. truncatus* individuals tend to fly longer distances than older individuals, which means that the pheromone trap catch range may be biased toward certain age classes. Lower flight activity of older compared with younger beetles was also found by Aslam et al. (1994) and Dowdy (1994) in laboratory experiments with the closely related, lesser grain borer, *Rhyzopertha dominica* (F.). Hence, pheromone trap catches may not be representative of the entire *P. truncatus* population, and although the mating status and sex of individuals caught in the pheromone traps were not determined in this study, it is therefore possible that the present model of *P. truncatus* flight activity mainly applies to young mated females.

Because of the constraints on pheromone trap catch interpretation mentioned above, the main purpose of the response surface regression analysis presented here was not to predict absolute pheromone trap catches but to determine the sensitivity of *P. truncatus* flight activity to a small number of environmental variables. Single-factor response of *P. truncatus* flight activity to, for instance, temperature is difficult to relate to ambient conditions, so it is important to include linear interactions among environmental variables in such models. The importance of including interactions was seen in the flight activity response to changes in daylength (Fig. 3). However, as pointed out by Turchin et al. (1991), multiple regression is problematic, compared with linear regression, be-

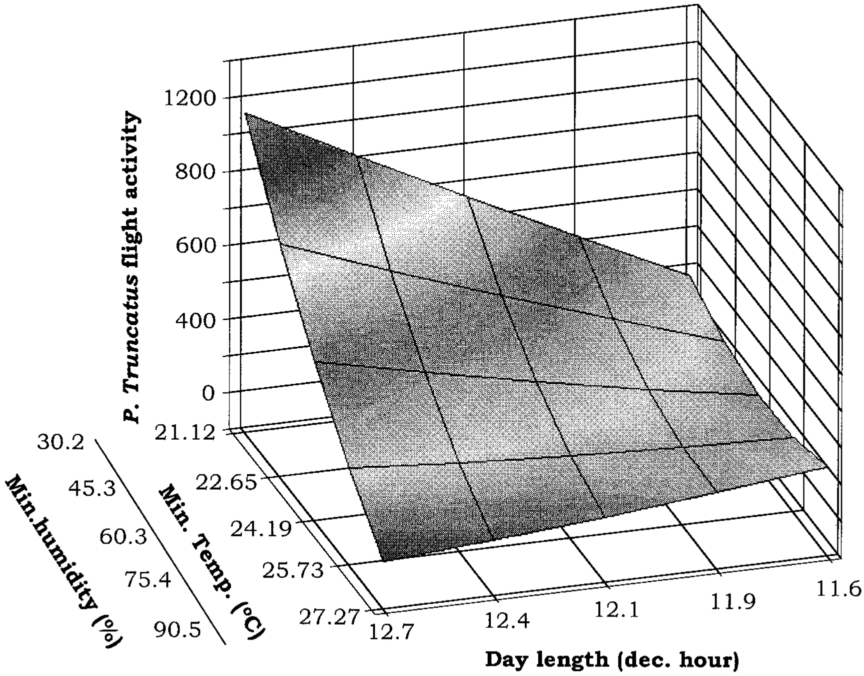

Fig. 3. Model-based evaluation of the sensitivity of *P. truncatus* flight activity (pheromone trap catches) to changes in daylength. Five values were chosen for daylength, minimum temperature, and minimum relative air humidity, and these values were equal to the mean ± one and two standard deviations (Table 1). The flight activity response was then determined when daylength was changed and minimum temperature and minimum relative air humidity were held constant at each of the five levels.

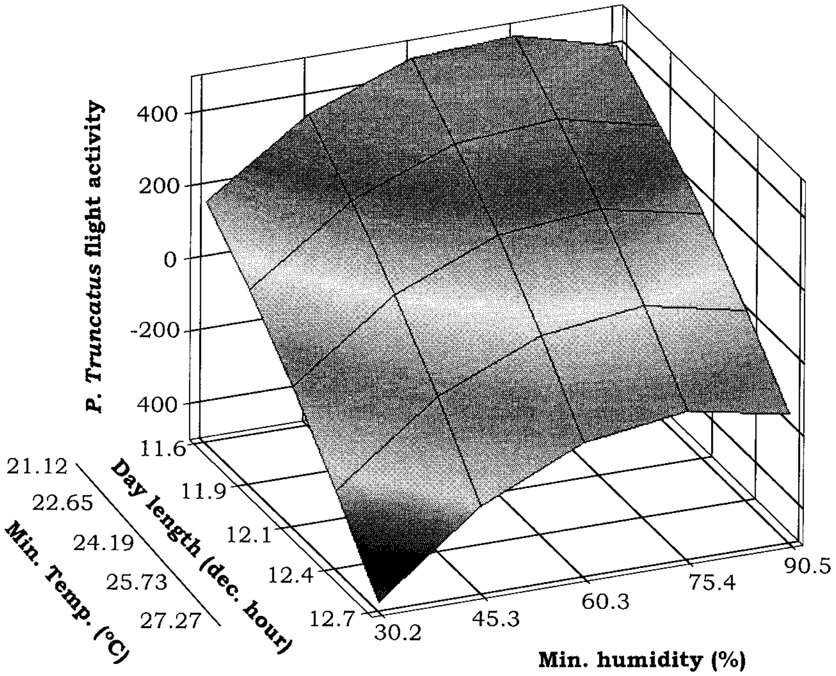

Fig. 4. Model-based evaluation of the sensitivity of *P. truncatus* flight activity (pheromone trap catches) to changes in daylength. Five values were chosen for daylength, minimum temperature, and minimum relative air humidity, and these values were equal to the mean ± one and two standard deviations (Table 1). The flight activity response was then determined when minimum relative air humidity was changed and minimum temperature and daylength were held constant at each of the five levels.

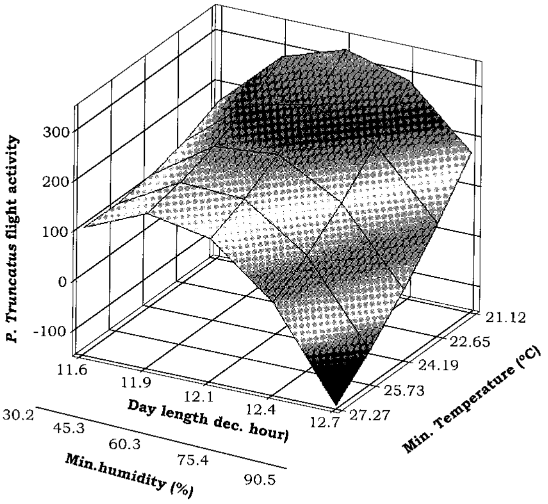

Fig. 5. Model-based evaluation of the sensitivity of *P. truncatus* flight activity (pheromone trap catches) to changes in daylength. Five values were chosen for daylength, minimum temperature, and minimum relative air humidity, and these values were equal to the mean ± one and two standard deviations (Table 1). The flight activity response was then determined when minimum temperature was changed and minimum relative air humidity and daylength were held constant at each of the five levels.

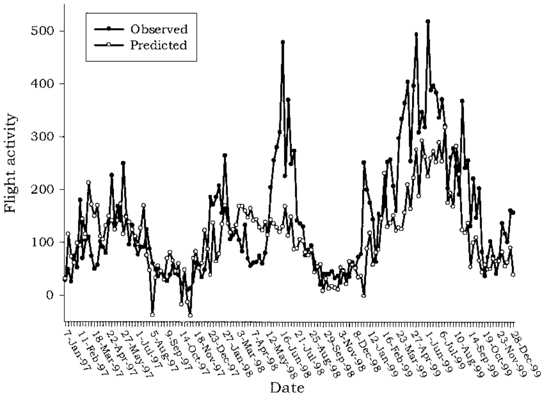

Fig. 6. Validation of the model for *P. truncatus* flight activity near Lokossa in southern Benin. Environmental variables for Lokossa were interpolated from meteorological stations in Cotonou and Bohicon. Observed *P. truncatus* trap catches correspond to the weekly mean of eight trap sites <25 km from Lokossa from 1997 to 1999.

cause the higher number of variables and interactions increases the likelihood of obtaining a significant fit by chance.

Generally, the dynamics of pheromone trap catches are determined by factors at four levels: (1) trap design and exposure, (2) spatial variance caused by site conditions, (3) variance in flight activity within a time-period shorter than one generation, and (4) variance in flight activity in periods longer than one generation. Borgemeister et al. (1997b) examined the influence of seasonal and weather factors on *P. truncatus* flight activity in southern Benin. They suggested that the first peak of the yearly bimodal *P. truncatus* flight activity pattern in southern Benin was associated with the time period during which maize stores were destocked and therefore disturbed, while the second peak was associated with phenology of unidentified forest substrates. However, in Lokossa in southwestern Benin, Borgemeister et al. (1997a) only showed a distinct bimodal *P. truncatus* flight activity pattern in two out of six seasons. A bimodal flight activity pattern was seen in 1998 for the pheromone traps in near Bohicon (Fig. 2) and Lokossa (Fig. 6). However, only one distinct peak in pheromone trap catches was found in 1997 in Lokossa and in 1999 in both Lokossa and Bohicon. Maize is an important staple food crop in southern Benin, consumed and available all year round. Data from a recent country-wide survey of maize stores in Benin in 1997 and 1998 included 17 stores from villages in southwestern Benin (Meikle et al. 2000). In these villages, two farmers stored their maize in June, seven farmers in July, eight farmers in August, while farmers who stored later than this were not included in the survey (Meikle unpublished data). Thus, the period of stocking varied considerably among farmers and was less of a discrete event than suggested by Borgemeister et al. (1997b).

The present model of *P. truncatus* flight activity showed that the environmental variables explained most of the variation in pheromone trap catches; 55% of the variance was explained by weekly means of environmental conditions (level 3, above), and only 8% by conditions changing on a yearly time scale (level 4). The remaining unexplained variation (37%) may be due to factors at levels 1 and 2, variables not included in the model, and stochasticity. Using a subset of the pheromone trap catches from the Lama forest included in this study, Nansen et al. (1999) showed that *P. truncatus* pheromone trap catches were spatially aggregated in 16 of the 21 weekly trap catches, and our unpublished data showed that this spatial aggregation pattern was positively correlated with the occurrence of specific vegetation types on trap sites. Borgemeister et al. (1997b) attributed 10% of the variance in pheromone trap catch to environmental conditions (mean daily temperature) and found 30% explained by the "year of trapping." However, although the analysis was similar to the one presented here, they included fewer variables and no interactions in their model. As indicated by the validation exercise, the parameters in the present model could only predict flight activity in a limited geographical area, southern Benin. However, the model was valid when site-specific coefficients for the four variables were used to predict *P. truncatus* flight activity in the more northern localities of Save and Parakou. But at the most northern location tested, Natitingou, the model lost its predictive power completely. The inability of the model to predict *P. truncatus* flight activity in northern Benin is either a weakness of the model, or it suggests that the flight activity may not be driven by the same environmental conditions in all agro-ecological zones. On the map of natural vegetation in Africa (U.S. CIA 1997) it is seen that Natitingou is located at the border between deciduous forest-woodland savanna, which covers the southern and central part of Benin, and brush-grass savanna. It is possible that more arid climate and vegetation pattern in the north is associated with a different flight activity pattern of *P. truncatus* compared with central and southern Benin.

Modeling of biological systems is an important working tool to quantify how well underlying interactions are understood. The present analysis suggests that simple modeling (only including linear and quadratic responses) is appropriate for prediction of *P. truncatus* flight activity, but it must be based on regional data sets to provide accurate predictions. Further research is needed to clarify how the presented model can be improved and to what extent the *P. truncatus* flight activity response to environmental conditions shows geographical variation. Regional models of pheromone trap catches may increase the understanding of the relationships between pheromone trap catches, flight behavior, and population density and thereby be considered an initial step in the development of early warning systems to local maize farmers. Long time series of pheromone trapping of *P. truncatus* flight activity in Kenya (Nang'ayo 1996) and Benin (Borgemeister et al. 1997a) have shown considerable yearly fluctuations, and much of this variation has so far been attributed to decreasing *P. truncatus* population density after releases of a natural control agent, *Teretrius nigrescens* (Lewis). With more knowledge about the *P. truncatus* flight activity response to environmental conditions, it becomes easier to assess the relative impact of, for instance, releases of natural enemies and/or changes in farming practices on the overall *P. truncatus* population dynamics. The response surface regression analysis outlined some overall trends in the relationship between environmental variables and flight activity of *P. truncatus:* (1) it was positively correlated with daylength when daily minimum temperature and relative air humidity were low, (2) it was positively associated with minimum relative air humidity when lower than 75%, (3) it was negatively associated with minimum temperature, (4) unexplained yearly variation was important for the predictive strength of the model, (5) interactions of environmental variables contributed substantially to the model fit, and (6) precipitation, both as mm rain and as number of rainy days, had little influence on *P. truncatus* flight activity. Although the model predicted well *P. truncatus* flight activity in southern Benin from which the model data originated, new coefficients for the same environmental variables were needed to predict the flight activity in central Benin.

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References Cited

Adda, C., C. Borgemeister, W. G. Meikle, R. H. Markham, I. Olaleye, K. S. Abdou, and M. O. Zakari. 1996. First record of the larger grain borer, *Prostephanus truncatus* (Coleoptera: Bostricidae), in the Republic of Niger. Bull. Entomol. Res. 86: 83–85.

Anonymous. 1986. Benin. Further distribution of the larger grain borer *Prostephanus truncatus* in West Africa. FAO Plant Protection Bull. 34: 213–214.

Aslam, A., D. W. Hagstrum, and B. A, Dover. 1994. The effect of photoperiod on the flight activity and biology of *Rhyzopertha dominica* (coleoptera: Bostrichidae). J. Kans. Entomol. Soc. 67: 107–115.

Bell, A., O. Mück, P. Mutlu, and H. Schneider. 1998. Der integrierte Nachernteschutz ist sein Geld wert!. Technical publication. Deutsche Gesellschaft für Zuzammenarbeit (GTZ), Eschborn, Germany.

Birkinshaw, L. A. 1998. Mate choice in *Prostephanus truncatus* (Horn) (Coleoptera: Bostricidae): the role of male-produced aggregation pheromone. Ph.D. thesis, University of Leicester, UK.

Boeye, J., A. Biliwa, H. U. Fischer, J. Helbig, and J. Richter. 1994. The dispersion pattern of *Teretriosoma nigrescens* Lewis (Col., Histeridae) after its release and monitoring of the occurrence of its host *Prostephanus truncatus* Horn (Col., Bostrichidae) in the natural environment in Togo, pp. 1098–1102. *In* E. Highley, E. J. Wright, H. J. Banks, and B. R. Champ (eds.), Proceedings of the 6th International Working Conference on Stored-product Protection, 17–23 April, Canberra, Australia. CAB, Wallingford, UK.

Bonzi, S. M. and C. Ntambabazi. 1993. Premier cas de grand capucin de maïs (*Prostephanus truncatus*) signalé au Rwanda. FAO Plant Prot. Bull. 4: 204–205.

Borgemeister, C., F. Djossou, C. Adda, H. Schneider, B. Djomamou, P. Degbey, B. Azoma and R. H. Markham. 1997a. Establishment, spread, and impact of *Teretriosoma nigrescens* (Coleoptera: Histeridae), an exotic predator of the larger grain borer (Coleoptera: Bostrichidae) in southwestern Benin. Environ. Entomol. 26: 1405–1415.

Borgemeister, C., W. G. Meikle, D. Scholz, C. Adda, P. Degbey, and R. H. Markham. 1997b. Seasonal and climate variables influencing the annual flight cycle of *Prostephanus truncatus* (Coleoptera: Bostrichidae) and its predator *Teretriosoma nigrescens* (Coleoptera: Histeridae) in Benin. Bull. Entomol. Res. 87: 239–246.

Borgemeister, C., A. Tchabi, and D. Scholz. 1998. Trees or stores? The origin of migrating *Prostephanus truncatus* collected in different ecological habitats in southern Benin. Entomol. Exp. Appl. 87: 285–294.

Bosque-Perez, N. A., R. H. Markham, and J. M. Falemisin. 1991. Occurrence of Larger grain borer *Prostephanus truncatus* in Burkina Faso. FAO Plant Prot. Bull. 39: 182–183.

Cogburn, R. R., W. E. Burkholder, and H. J. Williams. 1984. Field tests with the aggregation pheromone of the lesser grain borer (Coleoptera: Bostrichidae). Environ. Entomol. 13: 162–166.

Dick, K., D. P. Rees, K. K. Lay, and A. Ofosou. 1989. Occurrence of larger grain borer *Prostephanus truncatus* (Horn) in Ghana. FAO Plant Prot. Bull. 37: 132.

Dowdy, A. K. 1994. Flight initiation of lesser grain borer (Coleoptera: Bostrichidae) as influenced by temperature, humidity and light. J. Econ. Entomol. 87: 1714–1717.

Dunstan, W. R., and I. A. Magazini. 1981. Outbreaks and new records. Tanzania. The larger grain borer on stored products. FAO Plant Prot. Bull. 29: 80–81.

Fadamiro, H. Y. 1996. Free flight capacity determination in a sustained flight tunnel: effects of age and sexual state on the flight duration of *Prostephanus truncatus.* Physiol. Entomol. 22: 29–36.

Fisher, W. S. 1950. A revision of the North American species of beetles belonging to the family Bostrichidae. USDA Misc. Publ. 698.

Freund, R. J., and R. C. Littell. 1991. SAS system for regression. SAS Institute, Cary, NC.

Gilman, G. A. 1984. Presence et importance economique de *Prostephanus truncatus* et efforts supra-regionaux visant a empecher sa proliferation en Afrique, pp. 71–77. Workshop: "Le controle de l'infestation des denrées stockées par *Trogoderma granarium* et *Prostephanus truncatus,*" 10–15 December 1984, Lome, Togo. Deutsche Gesellschaft für Zuzammenarbeit (GTZ), Eschborn, Germany.

Harnisch, R., and S. Krall. 1984. Outbreaks and new records. Togo. Further distribution of the larger grain borer in Africa. FAO Plant Prot. Bull. 32: 113–114.

Hodges, R. J. 1994. Recent advances in the biology and control of *Prostephanus truncatus* (Coleoptera: Bostricidae), pp. 929–934. *In* E. Highley, E. J. Wright, H. J. Banks, and B. R. Champ (eds.), Proceedings of the 6th International Working Conference on Stored-product Protection, 17–23 April, Canberra, Australia. CAB, Wallingford, UK.

Hodges, R. J., G. Farrell, and P. Golob. 1996. Review of the Larger Grain Borer outbreak in East Africa—rate of spread and pest status. p. 29–41. In Farell, G., Greathead, A. H., Mill, M. G., & Kibata, G. N. (eds.) Management of Farm Storage Pests in East and Central Africa. Proceedings of the East and Central African Storage Pest Management Workshop 14–19 April 1996 Naivasha, Kenya. International Institute of Biological Control, Ascot, UK.

Hodges, R. J., D. R. Hall, J. N. Mbugua, and P. W. Likhayo. 1998. The responses of *Prostephanus truncatus* (Coleoptera: Bostrichidae) and *Sitophilus zeamais* (Coleoptera: Curculionidae) to pheromone and synthetic maize volatiles as lures in crevice and flight traps. Bull. Entomol. Res. 88: 131–139.

Holst, N., R. H. Markham, and W. G. Meikle. 1999. Integrated pest management of postharvest maize in developing countries. PURL (http:/www.purl.dk/net/9906–0408).

Kalivogui, K., and O. Mück. 1991. Larger grain borer (*Prostephanus truncatus*) (Horn) in Guinea. FAO Plant Prot. Bull. 39: 43.

Kega, V. K., and C. W. Warui. 1983. Prostephanus truncatus in coast province Kenya. Trop. Stored Prod. Inf. 46: 2.

Key, G. E., B. J. Tigar, E. Flores-Sanchez, and M. Vazquez-Arista. 1994. Response of to *Prostephanus truncatus* and *Teretriosoma nigrescens* to pheromone-baited flight traps, pp. 410–414. *In* E. Highley, E. J. Wright, H. J. Banks, and B. R. Champ (eds.), Proceedings of the 6th International Working Conference on Stored-product Protection, 17–23 April, Canberra, Australia. CAB, Wallingford, UK.

Malombo, C., J. Chakupuraka, A. Sumani, A. Sakala, K. Kashweka, C. Chisongo, and G. Chipabika. 1997. Present status of a biointegrated strategy for the control of the larger grain borer in Zambia, pp. 69–79. *In* C. Borgemeister, A. Bell, O Mück, and M. Zweigert (eds.), Proceedings from biological control to a systems approach in post-harvest, 13–15 October 1997, Cotonou, Benin. International Institute of Tropical Agriculture (IITA)/Deutsche Gesellschaft für Zuzammenarbeit (GTZ).

Meikle, W. G., N. Holst, P. Degbey, and R. Ossou. 2000. An evaluation of sequential sampling plans for the larger grain borer (Coleoptera: Bostrichidae) and the maize weevil (Coleoptera: Curculionidae) and of visual grain assessment in West Africa. J. Econ. Entomol. 93: 1822–1831.

Nang'ayo F.L.O. 1996. Ecological studies on larger grain borer in savannah woodlands of Kenya. Ph.D. dissertation, Imperial College, Silkwood Park, Berkshire, UK.

Nansen, C., S. Korie, and W. G. Meikle. 1999. CANOCO and SADIE–software packages for spatial analysis of pheromone trap catches of a maize storage pest and its biological control agent. J. Trop. For. Resour. 15: 146–158.

Pike, V., J.J.A. Akinnibagbe, and N. A. Bosque-Perez. 1992. Nigeria - larger grain borer (*Prostephanus truncatus*) outbreak in Western Nigeria. FAO Plant Protection Bull. 40: 170–173.

Ramírez-Martínez, M., A. Alba-Avila, and R. Ramirez-Zurbia. 1994. Discovery of the larger grain borer in a tropical deciduous forest in Mexico. J. Appl. Entomol. 118: 354–360.

Rees, D. P., R. R. Rivera, and F.J.H. Rodriguez. 1990. Observations on the ecology of *Teretriosoma nigrescens* Lewis (Coleoptera: Histeridae) and its prey *Prostephanus truncatus* (Horn) (Coleoptera: Bostricidae) in the Yucatan peninsula, Mexico. Trop. Sci. 30: 153–165.

Riwa, W. 1998. Report of the working group on priorities for IPM research, pp. 48–50. *In* W. G. Meikle and S. Smith (eds.), Proceedings of Entomopathology and stored product pest management workshop, 30 November–3 December 1998, International Institute of Tropical Agriculture (IITA). IITA, Cotonou, Benin.

SAS Institute. 1989. SAS/STAT user's guide, version 6, 4th ed., vol. 2. SAS Institute, Cary, NC.

Scholz, D. 1997. Dispersal and Host-finding behaviour of *Prostephanus truncatus* (Horn) (Coleoptera: Bostricidae). Ph.D. dissertation, Hannover University, Germany.

Scholz, D., C. Borgemeister, W. G. Meikle, R. H. Markham, and H-M. Poehling. 1997. Infestation of maize by *Prostephanus truncatus* initiated by male-produced pheromone. Entomol. Exp. Appl. 83: 53–61.

Shires, S. W. 1979. Influence of temperature and humidity on survival, development period and adult sex ratio in *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). J. Stored Prod. Res. 15: 5–10.

Tigar, B. J., G. E. Key, E. Flores-Sanchez, and M. Vazquez-Arista. 1993. Flight peridiocity of *Prostephanus truncatus* and longevity of attraction to synthetic pheromone. Entomol. Exp. Appl. 66: 91–97.

Turchin, P., P. L. Lorio, Jr., A. D. Taylor, and F. R. Billings. 1991. Why do populations of the southern pine beetle (Coleoptera: Scolytidae) fluctuate? Environ. Entomol 20: 401–409.

(U.S. CIA) U.S. Central Intelligence Agency. 1997. Natural vegetation of Africa (http://library.berkeley.edu/EART/maps/africa-veg.gif).

Vowotor, K. A., W. G. Meikle, J. N. Ayertey, C.Borgemeister, and R. H. Markham. 1997. Intra-specific competition between larvae of the larger grain borer, *Prostephanus truncatus* (Horn) (Col.: Bostrichidae) within maize grains. Insect Sci. Appl. 18: 171–175.

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