

Spatial Analysis of *Prostephanus truncatus* (Bostrichidae: Coleoptera) Flight Activity Near Maize Stores and in Different Forest Types in southern Benin, West Africa

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ABSTRACT Weekly *Prostephanus truncatus* (Horn) flight activity, measured as the density of captured beetles in pheromone baited traps, was monitored for 76 consecutive weeks at 16 sites inside the Lama forest in southern Benin and at four sites in maize farmland just outside the forest. *Prostephanus truncatus* flight activity was consistently higher and the flight activity pattern significantly different near maize stores than at sites inside the forest. Although *P. truncatus* is known to infest girdled branches of *Lannea nigritana* (Sc. Elliot) Keay, the *P. truncatus* flight activity was comparatively low at forest sites where this tree species dominated. The main peak in *P. truncatus* flight activity occurred earlier in the eastern part of the forest compared with other forest parts. Ordination analysis showed that comparatively higher flight activity in the eastern part of the forest was positively associated with the presence of teak plantations (*Tectona grandis* L. F.) at trap sites. The spatial distribution of weekly *P. truncatus* trap catches were found to be significantly aggregated during a 21-wk period, which largely coincided with the early increase in *P. truncatus* flight activity in the eastern part of the forest. Based on this evidence, it was suggested that *P. truncatus* individuals disperse from the eastern part of the forest to other forest parts and to nearby agricultural areas, rather than, as has been previously suggested, from maize stores to the forest environment.

KEY WORDS *Prostephanus truncatus*, pheromone trap catches, population ecology, spatial distribution, West Africa

MOST FIELD RESEARCH on insects pests focuses on their damage and population dynamics in fields and storage systems, while, for instance, their spatial distribution pattern and spatial migration patterns between crops and wild hosts are generally given less attention. Pheromone trapping of important storage pests has been used to document their occurrence on locations at a considerable distance from the nearest food-storage system including Lepidopteran storage pests, such as *Sitotroga cerealella* (Olivier) (Cogburn and Vick 1981, Vick et al. 1987), *Plodia interpunctella* (Hübner) (Vick et al. 1987, Doud and Phillips 2000), *Ephestia kuehniella* (Zeller), and *E. cautella* (Walker) (Cogburn and Vick 1981, Vick et al. 1987) and bostrichid storage pests, such as *Rhyzopertha dominica* (F.) (Cogburn et al. 1983, Fields and Phillips 1994) and *Prostephanus truncatus* (Horn) (Rees et al. 1990, Farrell and Key 1992, Nang'ayo et al. 1996, Tigar et al. 1993, Ramírez-

Martínez et al. 1994, Nang'ayo 1996, Borgemeister et al. 1998b, Farrell 2000). Pheromone trap catches in nonagricultural habitats are not easy to interpret and it is rarely known whether they reflect dispersal from storage systems to nonagricultural habitats or whether natural hosts support "wild" populations, which under certain conditions leave their natural host and become a potential threat to stored products. Analysis of the spatial variation in flight activity in different habitats helps to determine the relative importance of natural habitats as refuges for stored product pests and to understand the seasonal flight activity pattern measured using pheromone-baited traps. In addition, spatial analysis of flight activity may provide insight into variation in insect population density within a given environment, and to the relationship of the insect with alternative host distribution and phenology. Taylor (1984) considered the spatial distribution pattern of an organism as one of its most important ecological characteristics, because it tends to be more stable than the population density between generations and/or seasons.

Prostephanus truncatus is one of the most important insect pests on stored maize and cassava in Africa (Hodges 1994). The adaptation of *P. truncatus* to stored commodities is believed to be recent (Markham 1990), and the original host plants are

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found in Meso American forest environments (Fisher 1950). Chittenden (1911) stated that roots and tubers probably serve as the natural host for *P. truncatus*, but this has not been confirmed in the natural habitat. The only records of *P. truncatus* colonies in forest habitats describe the presence of *P. truncatus* larvae and adults in branches previously girdled by cerambycids in Mexico (Ramírez-Martínez et al. 1994) and southern Benin (Borgemeister et al. 1998a). Nang'ayo (1996) reported trapping *P. truncatus* in forests far from agricultural areas. The importance of girdled branches as hosts for *P. truncatus* in forest and savanna habitats is difficult to assess without complementary data on the abundance and spatial distribution of the girdled tree species. The ability of *P. truncatus* to reproduce and survive in forest habitats has been proposed as a serious constraint to eradication and/or control of this pest in maize stores (Ramírez-Martínez et al. 1994). More knowledge about the spatial distribution pattern of *P. truncatus* and its affinity to certain vegetation types may provide information on how and where to implement integrated pest management (IPM) strategies for this pest in nonagricultural areas.

In this study, we examined *P. truncatus* pheromone trap catches inside the Lama forest in southern Benin and near maize stores just outside the forest. A previous study of pheromone trap catches of *P. truncatus* in the Lama forest (Nansen et al. 1999) showed that catches were comparatively higher in the eastern part of the Lama forest compared with other parts, and this trend was not found to be related to the physical structure of the forest (e.g., tree density and size of trees). Instead, the spatial distribution of certain tree species and/or forest types was proposed as a possible explanation for the observed spatial distribution of beetle captures. The objectives of this study were to characterize the following: (1) how well pheromone trap catches near maize stores are correlated with the density of *P. truncatus* in the stores, (2) to what extent *P. truncatus* trap catches near maize stores follow the same seasonal pattern as trap catches in the forest environment (3) whether high or low pheromone trap catches of *P. truncatus* in the forest were associated with the occurrence of certain vegetation types on trap sites, and (4) how well the overall spatial distribution pattern of *P. truncatus* trap catches matches the distribution of vegetation types in the Lama forest.

Materials and Methods

Occurrence of *P. truncatus* in Maize Stores and in Nearby Pheromone Traps. The relationship between pheromone trap catches and *P. truncatus* population density is not known in detail, but five published data sets from southern Benin were used to examine the relationship between *P. truncatus* population density in maize stores and pheromone trap catches within 1 km of the maize stores. In Borgemeister et al. (1994), 12 small-holders' maize stores were constructed in the Mono Province in Southwestern Benin, and all stores were sampled every 3 wk from October 1992 to May 1993 (12 sampling occasions). At each sampling oc-

casional, 20 maize cobs were collected from each maize store and the density of *P. truncatus* per kilogram of maize was determined. As described in Borgemeister et al. (1997), similar surveys of small-holders' maize stores were conducted for the same time period in 1993–1994 (12 sampling occasions) and 1994–1995 (eight sampling occasions). Workers at the International Institute of Tropical Agriculture (IITA) in Cotonou conducted continuous pheromone trapping of *P. truncatus* in the Mono Province from 1992 to 2000, and the occurrence of *P. truncatus* in maize stores was compared with the *P. truncatus* pheromone trap catches within 1 kilometer and during the same week the stored-maize samples were collected. From September 1994 to May 1995, Meikle et al. (1998a) sampled 16 experimental maize stores at the IITA station in southern Benin at 4-wk intervals (eight sampling occasions). At each sampling occasion 60 maize cobs were collected from each maize store and the *P. truncatus* density per kilogram of maize determined. From October 1995 to June 1996, Meikle et al. (1998b) sampled experimental maize storage systems at the same site, again at 4-wk intervals (10 sampling occasions). At each sampling occasion, 60 maize cobs were sampled from each of 16 maize stores. *P. truncatus* density in the maize stores on the IITA station was compared with weekly *P. truncatus* pheromone trap catches (<300 m from experimental stores) during the same week the maize samples were collected.

Study Area. The Lama forest is located at 6° 55.8' to 6° 58.8' N and 2° 4.2' to 2° 10.8' E in southern Benin (Fig. 1). To examine the spatial distribution pattern of *P. truncatus* inside the forest, we conducted weekly pheromone trapping at 16 trapping sites inside the forest and at four sites ≈50 m from small-holders' maize stores of the "Adja" type (Meikle et al. 1998a) <1 km from the forest perimeter. Hereafter, trap sites located in the forest were referred to as "forest traps" and trap sites located near maize stores were referred to as "maize traps."

All traps were installed on 23 September 1998, and trapping continued at all sites until 22 March 2000. Three weekly pheromone trap catches from all 20 sites were lost (from 21 January 1999–1993 February 1999 and 12 January to 19 January 2000). Hence, trapping data from 76 wk are included in this study. Sticky traps (Pherocon II, Trécé, Salinas, CA) and *P. truncatus* lures (Agrisense-BCS, Pontypridd, UK) were used, and both sticky traps and pheromone lures were changed weekly. With weekly pheromone trap catches exceeding 1,000 individuals, saturation of the sticky surface inside traps may occur if the same trap is used for more than a week. Although *P. truncatus* pheromone lures can be used for up to 8 wk (Agrisense-BCS, Pontypridd, UK), new lures were always used in new traps. At all sites, the traps were placed 1.5 m above the ground at well exposed locations. The geographical position of forest trap sites was determined from the coordinates of the junctions of east-west forest transects with the road around the forest as reference points and by measuring the distance of trap sites to the forest perimeter.

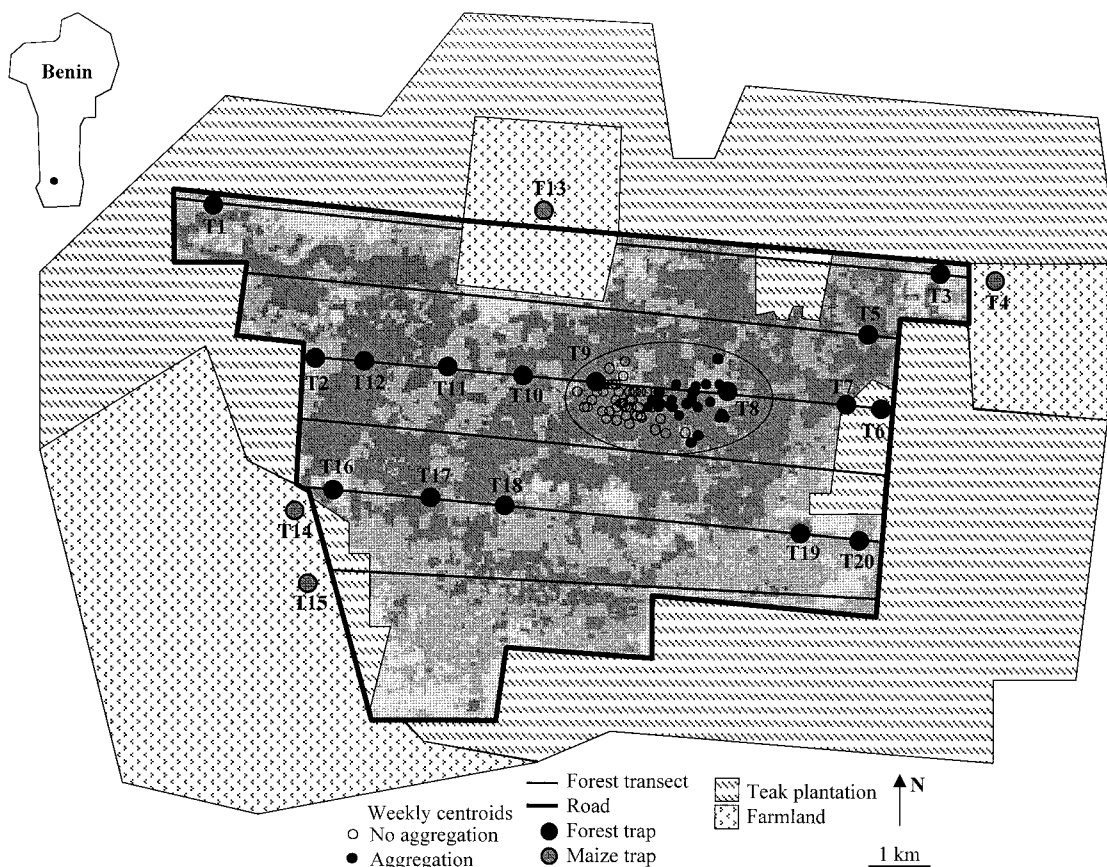


Fig. 1. Lama Forest in Southern Benin. Density of forest vegetation is indicated by increasingly dark gray tones. Pheromone traps inside the forest (black circles) were placed along transects (lines) in east-west direction, and traps near maize stores were placed in open farmland (gray circles). Smaller dots in the north eastern part of the forest denote the theoretical centroids (spatial mean) of pheromone trap catches for all 76 wk.

Vegetation on Trap Sites. The Lama forest is composed of forest types consisting of pioneer vegetation on former farmland, teak plantation, derived savanna vegetation and dense semideciduous forest. Nansen et al. (2001) identified five nondiscrete forest types (Ftype) in the Lama forest, and the following indicator tree species were identified:

Derived Savanna. *Lonchocarpus sericeus* (H.B.K.), *Phyllanthus discoideus* (Müll. Arg.), and *Albizia zygia* (J. F. Macbr.) (Ftype 1).

Formerly Cultivated farmland or open Woodland. *Ceiba pentandra* (Gaertn.), *Anogeissus leiocarpus* (Guill. And Perr.), *Ficus capensis* (Thunb.), *L. nigritana* (Ftype 2).

Woodland. *Azelia africana* (Sm.) and *Mimosops andongensis* (Hiern) (Ftype 3).

Thicket. *Dialium guineense* (Willd.), *Drypetes floribunda* (Hutch.), *Diospyros mespilliformis* (Hochst), and *Ochna membranacea* (Oliv.) (Ftype 4).

Dense Forest. *D. floribunda*, *Pancovia bijuga* Willd., and *Cassipouira congoensis* (R. Br.) (Ftype 5).

Forest trap sites were selected to include samples from all five forest types and to ensure sufficient distance between trap sites. Farrell and Key (1992) sug-

gested that pheromone traps should not be placed closer than 340 m to avoid interaction between traps. In the current study, trap sites were at least 500 m apart.

Ordination of Pheromone Trap Sites in the Forest and in Maize Growing Areas. Ordination techniques available in the software package, CANOCO (CANOnical Community Ordination, Ithaca, NY) for Windows version 4.02, were used to examine the relationship between trap sites based on weekly *P. truncatus* flight activity. Comprehensive descriptions of the ordination techniques is available in Jongman et al. (1995) and ter Braak (1994 1996). ter Braak (1996) considered two types of ordination techniques—indirect and direct. Indirect ordination is based on a single data matrix most commonly with sites and occurrence of species (in this case, sites and weekly *P. truncatus* flight activity) and is used to interpret the relationship between sites in a two-dimensional space based only on descriptive variables. In direct ordination, the relationship between sites and descriptive variables is also examined in a two-dimensional space, but it is “restricted” by an additional matrix of environmental data. Direct ordination is, therefore, based on both

Table 1. Environmental variables for the ordination analysis of *P. truncatus* flight activity at 16 trap sites inside in the Lama forest and at four trap sites near maize stores just outside the forest

Trap	North ^a (dec deg)	East ^a (dec deg)	Dist, km ^b	Mean ^c weekly catch	Vegetation on pheromone trap sites ^d					
					Teak	Ftype1	Ftype2	Ftype3	Ftype4	Ftype5
T1	6.9785	2.0823	0.30	204.7	0	1	3	0	0	0
T2	6.9599	2.0958	0.00	164.9	2	1	1	0	0	0
T3	6.9706	2.1772	0.25	256.4	0	0	4	0	0	0
T5	6.9629	2.1649	0.35	188.3	0	0	0	0	1	3
T6	6.9545	2.1674	0.00	281.1	4	0	0	0	0	0
T7	6.9548	2.1629	0.50	246.1	3	1	0	0	0	0
T8	6.9560	2.1472	2.25	140.8	0	0	4	0	0	0
T9	6.9573	2.1305	4.10	87.7	0	0	2	2	0	0
T10	6.9579	2.1229	3.00	157.5	0	0	2	1	1	0
T11	6.9589	2.1093	1.50	213.7	0	1	2	1	0	0
T12	6.9593	2.1035	0.85	96.5	0	0	0	1	2	1
T16	6.9434	2.0969	0.30	167.7	0	0	0	0	1	3
T17	6.9416	2.1123	2.00	115.7	0	0	0	2	1	1
T18	6.9406	2.1213	3.00	87.8	0	0	0	1	1	2
T19	6.9368	2.1542	1.40	173.6	0	4	0	0	0	0
T20	6.9356	2.1643	0.28	284.7	3	1	0	0	0	0
T4 (m) ^e	6.9704	2.1800	0.00	396.1	0	0	0	0	0	0
T13 (m)	6.9769	2.1248	0.00	244.3	0	0	0	0	0	0
T14 (m)	6.9500	2.0900	0.00	400.7	0	0	0	0	0	0
T15 (m)	6.9390	2.0900	0.00	653.3	0	0	0	0	0	0

^a The geographical position trap sites is presented in Fig. 1. Latitude (north) and longitude (east) are presented in decimal degrees.

^b Distance of forest traps from the nearest forest perimeter.

^c Mean number of *P. truncatus* individuals caught during 76 wk of pheromone trapping.

^d For each forest trap site, four vegetation scores were distributed according to visual assessment of dominant vegetation types in a range of 75 m from each trap site.

^e Maize stored are denoted with an "m".

descriptive variables and the inferred environmental variables (Jongman et al. 1995, ter Braak 1996). In ordination, iterative procedures are used to organize the data set along variance gradients (often expressed in standard deviations). In the CANOCO procedure, each descriptive variable is standardized and their sequence does not influence the ordination. Therefore, the same ordination result would have been obtained if the weekly trap catch data had been randomly ordered rather than chronologically ordered. Ordination analysis is most commonly presented using the two principal gradients (those gradients which explain the largest part of the total variance), and in this two-dimensional space the proximity of points reflects their level of similarity. The choice of appropriate ordination technique depends on the total variance in the dataset, and as Jongman et al. (1995) pointed out, unimodal models, such as detrended correspondence analysis, are more general than linear models. If the length of the principal axes in the initial detrended correspondence analysis does not exceed four standard deviations, a linear model (e.g., principal component analysis) may be used; otherwise, unimodal models are more appropriate.

Absolute magnitudes of pheromone trap catches were used for this analysis. A preliminary detrended correspondence analysis of the *P. truncatus* flight activity showed that ordination based on a unimodal response model was the most appropriate. A canonical correspondence analysis (direct ordination) was conducted to outline the overall similarity of *P. truncatus* flight activity among sites according to the following 11 environmental variables (listed in Table 1): (1)

latitude in decimal degrees of trap sites (North), (2) longitude in decimal degrees of trap sites (East), (3) Distance denoted distance of forest trap sites from nearest forest perimeter (maize traps were given the value zero), (4) a dichotomous variable, Forest (not listed in Table 1), to distinguish forest traps and maize traps (maize traps = 0 and forest traps = 1), (5–9) five variables representing the occurrence of each of the forest types at trap sites (Ftype1–5). The forest type variables were generated based on a visual assessment of the forest vegetation in a range of ≈ 75 m from each trap site. At each trap site, four vegetation scores were distributed: if only one forest type was present, all four scores were given to this forest type, if two forest types were equally abundant they were given two scores each, and so forth. The forest classification by Nansen et al. (2001) did not include the part of the Lama forest dominated by teak plantation (*Tectona grandis* L. F.). Hence, a sixth vegetation type, Teak, was included representing teak plantation. A variable denoting the mean weekly trap catch was also included in the analysis (Mean). Significance of environmental variables was determined using 199 unrestricted permutations in a Monte Carlo test ($\sigma = 0.05$).

Spatial Distribution Pattern. Detailed descriptions of SADIE (Spatial Analysis of Distance Indices, Harpenden, UK) for MS-Dos are available in Perry and Hewitt (1991), Perry (1995), and Perry et al. (1996). SADIE is used to determine the spatial pattern of a population by measuring the total effort that must be expended to move the data to extreme arrangements (regular, random or aggregated). The effort is quantified by the distance needed to move the points of

interest (in this case weekly trap catches) to a completely regular spatial distribution. The degree of non-randomness is quantified by comparing the observed spatial pattern with interactive rearrangements in which the sampled counts are randomly redistributed among the units by permutation. Absolute magnitudes of trap catches were used for this analysis, and the spatial distribution pattern was determined for each of the 76 wk of pheromone trapping at the 16 forest trap sites, while the four maize traps were excluded. The theoretical centroid for each week was calculated, and it corresponds to the weighted linear mean of trap catches in which distance between trap sites is the weighting factor. Hence, the theoretical centroid provides a simple measure of the spatial arithmetic mean (Korie et al. 1999) of weekly *P. truncatus* flight activity.

Results and Discussion

Relationship Between *P. truncatus* Flight Activity and Population Density. There is evidence that pheromone traps are selective and mainly attractive to certain members of the total *P. truncatus* population: Borgemeister et al. (1998b) in southern Benin, Nang'ayo (1996) in Kenya, and Birkinshaw (1998) in south eastern Ghana found that 60–70% of the *P. truncatus* caught in pheromone traps were females. In addition, Fadamiro (1996) found that young individuals tend to fly longer distances than older individuals, which means that the pheromone trap catch range may be biased toward certain age classes. Such selectivity in the trap captures may have an impact on the interpretation of pheromone trap catches, so the first step in the spatial analysis of *P. truncatus* in the Lama forest was to examine to what extent these catches were correlated with beetle density in nearby maize stores. A significant correlation would indicate that, despite the selectivity of pheromone traps as sampling tools, trap catches presumably represent a more or less constant percentage of dispersing beetles within a local population. Population density in stores and nearby trap catches for four of the maize store data sets (not for the data set from the Mono Province 1994–1995), and the regression analysis for all observations combined, were found to be significantly correlated (Fig. 2). Based on this result, we assumed that trap catches were directly proportional to *P. truncatus* population density in the environment around the trap site.

Flight Activity in Forest and Near Maize Stores. Of the 1,520 pheromone trapping occasions (20 trap sites \times 76 wk) in and around the Lama forest, *P. truncatus* was caught in all except 2. The highest weekly *P. truncatus* trap catches (2,115 individuals) and highest mean weekly trap catches were obtained in a maize trap (trap site 15) on the southwestern side of the forest (Fig. 3). Weekly *P. truncatus* flight activity above 1000 individuals was obtained at five forest traps (traps 1, 3, 6, 11, and 20) and at all four maize traps, while the flight activity at three trap sites (traps 9, 17, and 18) never exceeded 500. The lowest mean flight activity was obtained from forest trap sites in the

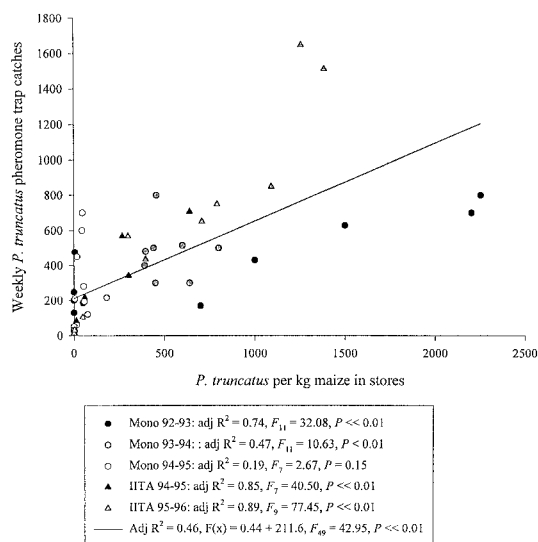


Fig. 2. Regression analysis of the *P. truncatus* population density in small-holders' maize stores and pheromone trap catches within a 1-km range from the stores. All five data sets originate from either a village in the Mono Province or the IITA station both located in southern Benin. Each data set represents consecutive observations over a 7- to 9-mo period.

central part of the forest (Figs. 1 and 3). Mean trap catches were 423.6 at the four maize traps and 179.2 at the 16 forest traps. The four trap sites with lowest averages (traps 9, 18, 12, and 17) had the lowest *P. truncatus* trap catches for more than half of the total trapping period and the six trap sites with highest mean catches (traps 6, 20, 13, 14, 4, and 15) had the highest *P. truncatus* flight activity in >47% of the total trapping period. Thus, high or low mean *P. truncatus* flight activity was due to a consistent pattern of comparatively high or low flight activity between sites throughout the trapping period.

***Prostephanus truncatus* Flight Activity Near Girdled *L. nigritana* Trees.** The vegetation at trap site 8 was characterized as forest type 2 (Table 1), and *L. nigritana* trees dominated the vegetation on that site and most of them had been girdled at at least one point on the tree by cerambycids. Forest trap 8 had the fifth lowest mean *P. truncatus* flight activity (Fig. 3). Borgemeister et al. (1998a) found *P. truncatus* larvae and adults in girdled branches of *L. nigritana* in the Lama forest and suggested that this may be an important natural host. Assuming that *P. truncatus* flight activity is positively associated with population density in the immediate vicinity of the trap, the comparatively low pheromone trap catches on this site suggested that this host plays a minor role in *P. truncatus* population dynamics in the Lama forest. *Lannea nigritana* trees are found throughout the Lama forest, but this tree species was either absent or found in very small numbers on the trap sites where the highest *P. truncatus* flight activity was observed (Nansen 2000).

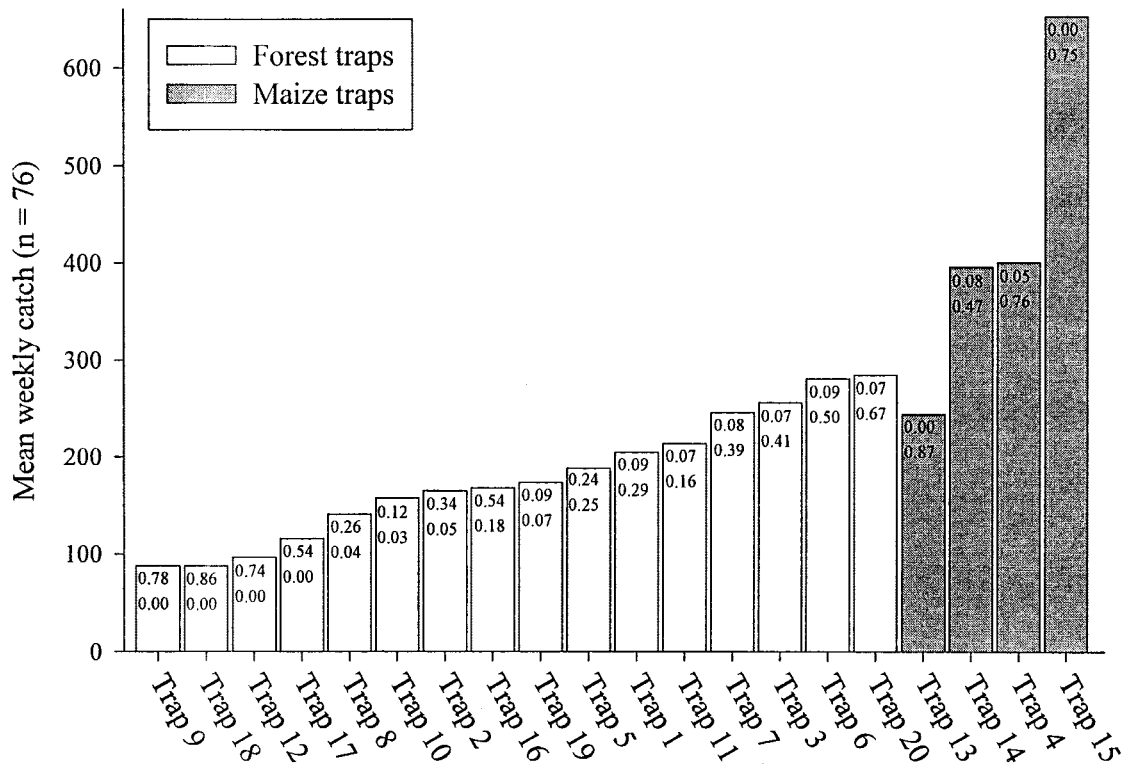


Fig. 3. Mean *P. truncatus* flight activity during 76 wk based on pheromone trap catches in the Lama forest in Southern Benin. White bars denote forest traps (inside the forest) and gray bars denote maize traps (placed near maize stores just outside the Lama forest). Location of trap sites is presented in Fig. 1. Upper number inside bars represents the fraction of the 76 wk of trapping in which the weekly pheromone trap catch was among the five lowest of the 20 trap sites; the lower number inside bars represents the fraction of the 76 wk of trapping in which the weekly pheromone trap catch was among the five highest of the 20 trap sites.

Ordination of Weekly Pheromone Trap Catches.

The environmental variables (except the variable Forest, used to analyze the difference between maize traps and forest traps) used in the ordination analysis are presented in Table 1. A canonical correspondence analysis of all 20 trap sites (not shown) revealed that the following environmental variables explained a significant part of the total variance (in order of importance): East ($F = 7.46$, $P < 0.01$), forest ($F = 5.31$, $P < 0.01$), North ($F = 2.05$, $P = 0.04$), and forest type 2 ($F = 1.73$, $P = 0.05$). The environmental variables, Forest types 1, 3, 4, 5, Teak, Distance, and Mean, did not explain a significant part of the variance in *P. truncatus* flight activity. The dichotomous variable Forest separated maize traps from forest traps, and that it was significant indicates that the flight activity pattern in the two environments was different. A second canonical correspondence analysis with the same environmental variables (the variable, forest, was excluded) was conducted in which only the 16 forest trap sites were included (Fig. 3). The significant environmental variables were in order of importance: East ($F = 5.07$, $P < 0.01$), Teak ($F = 1.93$, $P = 0.01$), and Forest type 5 ($F = 2.21$, $P = 0.03$). The remaining environmental variables (North, Forest types 1, 2, 3, 4, Distance, and Mean) did not explain a significant part of the variance

in *P. truncatus* flight activity. In Fig. 4, the forest traps were generally separated into two groups: four traps (denoted group 1) were all located in the eastern part of the forest, and with the exception of trap site 5, teak was the dominant vegetation type on these trap sites (Table 1). As seen from Fig. 3, high mean *P. truncatus* flight activity was obtained on trap sites belonging to group 1. The second cluster of forest traps occurred along the positive side of the principal axis, CCA1, in Fig. 4, and these trap sites were located in the central and western part of the forest. Comparatively low mean *P. truncatus* flight activity was obtained on forest trap sites in group 2 (Fig. 3).

Teak Plantation on Pheromone Trap Sites. Teak was present mainly at trap sites in the eastern part of the forest, so the significance of the Teak variable could be due to covariance of the variables, Teak, and East. A partial canonical correspondence analysis (not shown) of the 16 forest trap sites was conducted in which the explanatory strength of the teak variable was examined after removing the variance attributed to the eastern position of trap sites, essentially removing the effects of east. The Teak variable was significant ($F = 1.93$, $P = 0.02$), indicating that the contribution of the Teak variable was likely to be independent from the East variable.

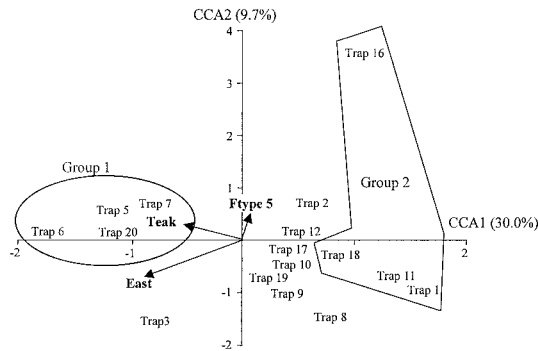


Fig. 4. Canonical correspondence analysis of *P. truncatus* flight activity during 76 wk at the 16 forest traps in the Lama forest in Southern Benin. Weekly pheromone trap catches were descriptive variables for the relationship between trap sites. Eleven variables (Table 1) describing spatial location and the vegetation on trap sites were examined as explanatory for the between-site variance in *P. truncatus* flight activity, and three variables explained a significant part of the total variance: (1) East: denotes the eastern coordinate of trap sites, (2) Teak: denotes the occurrence of planted teak, and (3) Forest type 5: denotes the occurrence of a dense semideciduous forest type with the following indicator tree species: *Drypetes floribunda*, *Pancovia bijuga*, and *Cassipouira congoensis*. Axes are in standard deviations; and the percentage values denote the amount of variation explained by the principal axes, CCA1 and CCA2.

Spatial Variation in Main Peak Flight Activity. The seasonal fluctuations in *P. truncatus* trap catches at maize store sites were similar in pattern to trap catches at forest sites from September 1998 to May 1999 and from December 1999 to February 2000 (Fig. 5). Nansen et al. (2002) used the pheromone trap catches included in this study and additional data from southern Benin to determine the sensitivity of *P. truncatus* flight activity to environmental variables. They developed a *P. truncatus* flight activity model based on daylength, minimum relative air humidity, and minimum temperature and a discrete yearly time-variable. The combination of these four variables explained 63% of the variance, when the model was validated with a second set of pheromone trap catches also from southern Benin. The flight activity pattern of *P. truncatus* on a regional level is apparently driven by regional climate conditions, similarly, environmental conditions on trap sites seem likely to be responsible for smaller-scale variation in the seasonal flight activity (Nansen et al. 2002). Forest traps were placed in one of two groups according to their location in the CCA graph (Fig. 4), and the mean trap catches of those groups were compared with mean maize trap catches. Weekly mean *P. truncatus* flight activity at forest sites 9 and 10 from the center of the Lama forest were also included in Fig. 5a for comparison. Most of the minor peaks coincided for the three groups of forest trap sites, but the main peak in *P. truncatus* flight activity occurred several weeks earlier (late April 1998) in the eastern than in the central and western forest parts. *Prostephanus truncatus* flight activity near maize stores

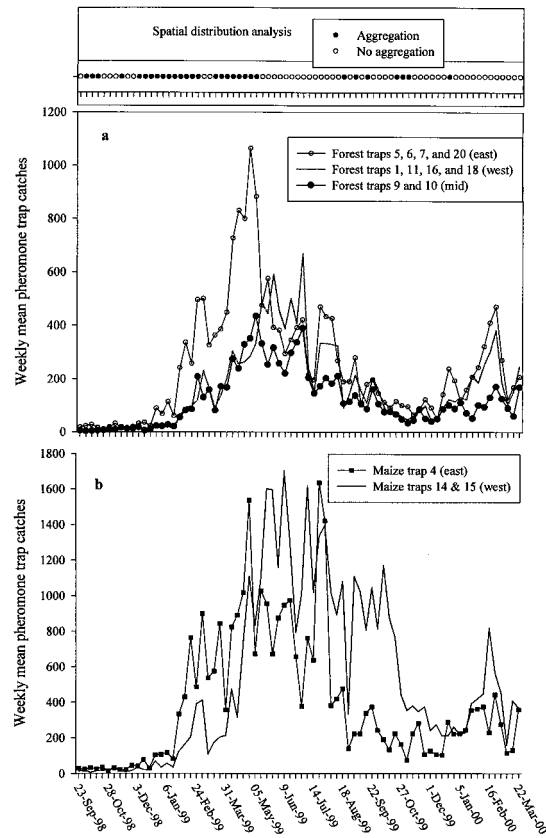


Fig. 5. Mean *P. truncatus* flight activity for three groups of pheromone trap sites in the eastern, central and western parts of the Lama forest in southern Benin during 76 wk (a), and near maize stores on the eastern and western sides of the Lama forest (b). The circles on top denote the weekly results from the spatial distribution analysis for each of the 76 wk of pheromone trapping: nonsignificant aggregation (open circles), significant aggregation (filled circles).

(Fig. 5b) was characterized by high amplitude of weekly fluctuations, so the seasonal pattern was less distinct than observed in the forest. The *P. truncatus* flight activity near maize stores and in the forest were characterized for the same time period with low flight activity until January 1999, when the pheromone trap catches, especially on the eastern side, started to increase. The maize trap on the eastern side of the forest seemed to reach a high level of *P. truncatus* flight activity slightly earlier than maize traps on the western side of the forest. Wind direction and speed were not measured inside the forest, but data from a weather station in Bohicon (18 km north of the Lama forest) showed that the predominant wind direction was south or southwest with wind speed between 0 and 7 knots. However, on most days wind speed was low (0–3 knots) and probably more diffuse inside the forest. It is, therefore, difficult to believe that the combination of wind speed and direction is the only explanation for the earlier peak in *P. truncatus* flight activity in the eastern part of the forest.

Spatial Distribution Pattern. In Fig. 1, the theoretical centroids of weekly pheromone trap catches generated in the SADIE analysis represent the spatial mean of the *P. truncatus* flight activity in each of the weeks. If the *P. truncatus* flight activity had fluctuated independently between trap sites, the distribution of these centroids would have been scattered randomly around in the forest. Instead, they were all located in the northeastern part of the Lama forest, because of the consistently higher flight activity in this forest part. Each set of the weekly pheromone trap catches was examined to determine whether it represented a spatially aggregated distribution, and this was found in 30 of the 76 wk of trapping, mainly from December 1998 to May 1999 (Fig. 5). Spatial aggregation suggests an association of the beetles with a particular part of the trapping area. During this period of aggregation, *P. truncatus* trap catches in teak dominated vegetation in the eastern part of the forest (forest traps 6, 7, and 20) increased considerably. One possible course of events is that, after this main peak in flight activity in the eastern part of the forest, aggregated populations or subpopulations then disperse to other forest parts and to nearby agricultural areas, which caused the observed change in spatial distribution to become a more homogeneous pattern. Infestations of maize stores by *P. truncatus* may, therefore, be related to beetle dispersal from nearby forest environments.

General. Although *P. truncatus* is known to attack previously girdled branches of *L. nigriflora*, the *P. truncatus* flight activity was comparatively low at forest sites where this tree species was important. Wind patterns may at least partially explain the slightly earlier peak in *P. truncatus* flight activity in the eastern part of the forest, but they would not explain the overall higher flight activity in that part of the forest. *P. truncatus* flight activity was characterized by a time period of 21 wk with significant spatial aggregation in the eastern part of the forest, during which flight activity increased almost monotonically. Teak was abundant at most, but not all, forest trap sites where comparatively high *P. truncatus* flight activity was observed, but the exceptions (e.g., forest trap 2) suggest that the presence of teak alone is not the explanation for high *P. truncatus* flight activity. Additional factors, which were not examined here, include the age of the teak plantation, soil conditions or tree-stressing factors. Such factors may have varied between parts of the teak plantation and created local differences in host susceptibility. More trapping data from other forest environments are needed to confirm the possible relationship between high *P. truncatus* flight activity and the presence of teak on trapping sites. Based on these results, laboratory and field experiments are being conducted to characterize the susceptibility of potential forest host plants in the Lama forest, including teak wood, roots and seeds, to *P. truncatus*.

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