

Quantitative analysis of temperature, relative humidity, and diet influencing development of the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae)

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Abstract. Data from three published studies on the development of *Prostephanus truncatus* (Horn) reared at constant temperatures and relative humidities (RH) were reanalysed to provide new information and quantitative description needed for predicting developmental times or rates in different environments. Models fitted to the temperature-dependent development data were used for comparing developmental times among insect stages, relative humidities, diets and studies. Development of the eggs and pupae was similar at 40%, 70%, 80%, and 90% RH. Significant differences were detected between studies in the egg hatch to adult development and larval development, attributable, in part, to differences in the degree of compaction of ground maize used for rearing insects. For all life stages the temperatures for minimum (T_{min}) and maximum (T_{max}) developmental rates, and degree-days above T_{min} required for completion of development, were estimated. The linear degree-day and nonlinear models presented here could be used for predicting *P. truncatus* development in the field. In conjunction with age-specific fecundity and adult longevity data, these development models will be valuable in predicting population trends of *P. truncatus* in the field. Predicting development and population trends is important for accurately timing insect sampling programmes and control tactics.

1. Introduction

The larger grain borer, *Prostephanus truncatus* (Horn) has long been recognized as a common but minor pest of farm-stored maize in Mexico, Central and South America, and as a sporadic pest in southern United States (Wright, 1984). During early 1980s, *P. truncatus* was introduced into parts of East and West Africa, where it has now become established as the most destructive pest of farm-stored maize and dried cassava (Hodges *et al.*, 1983; Krall, 1987; McFarlane, 1988). In Africa this pest was first detected during 1980 in the Tabora region of Tanzania (Hodges *et al.*, 1983). *P. truncatus* is now widely distributed in Tanzania, and has spread via primary or secondary introductions to parts of other African countries such as Kenya, Burundi, Zaire, Togo, Benin, Uganda, and Ghana (Schulz and Laborius, 1987; Rees *et al.*, 1990). In Togo, insect-related dry weight losses of local maize varieties during 8 months of storage prior to the occurrence or introduction of *P. truncatus* averaged 5.5%. Under the same conditions and duration of storage these losses averaged 44.8% after the appearance of *P. truncatus* (Krall, 1987). Such high grain weight losses in farm-stored maize due to *P. truncatus* infestations have also been observed in Tanzania (Hodges *et al.*, 1983). *P. truncatus* is now

considered a major threat to maize-producing regions of Africa. Hodges (1984) and Rees *et al.* (1990) have discussed some ecological and biological reasons for the establishment, rapid spread, and destructive nature of this pest in Africa compared with Central America and Mexico. Current chemical control methods and prospective pest management strategies for containing the spread of *P. truncatus* in Africa have been reviewed by McFarlane (1988).

P. truncatus can infest and breed on cob as well as shelled maize and dried cassava (Bell and Watters, 1982; Hodges *et al.*, 1983; Subramanyam *et al.*, 1987). Rees *et al.* (1990) have captured adults of *P. truncatus* in forest, henequen plantation, and dry scrubland habitats devoid of maize and cassava. The presence of *P. truncatus* in these habitats suggests that the pest is also able to survive on several alternative host plants besides maize and cassava (Rees *et al.*, 1990). Adults cause greater damage to cob than shelled maize because the kernels are more stable on the cob (Cowley *et al.*, 1980). Adults bore into wooden structures, maize husks, maize core and kernels. Grain damage is primarily due to tunnelling by adults, resulting in the production of large amounts of maize flour. The tunnels in the grain serve as oviposition sites (Howard, 1984), and the flour serves as a food source for emerging larvae. Shires (1980) reported that, on average, 68% of all eggs of a female are laid inside maize kernels where development of the immatures is completed.

Shires (1979) studied the development of *P. truncatus* from egg hatch (0–1-day-old larva) to the adult stage when reared on loosely compacted ground maize (maize flour) at 22–35°C and 50%, 60%, 70%, and 80% relative humidity (RH). Shires (1980) also reported developmental times for the egg, larval, and pupal stages of *P. truncatus* at 32°C and 80% RH. Bell and Watters (1982) reported developmental times for the eggs, larvae, and pupae reared on tightly compacted ground maize over a broad range of constant temperatures (18–37°C) at 40%, 70%, 80%, and 90% RH. They also studied the egg to adult development of *P. truncatus* at 22–35°C and 70% RH inside whole maize kernels. In all these studies, linear or nonlinear regression models were not fitted to the development data.

Linear and nonlinear regression models can be used to describe the effects of environmental variables on development of insect species (e.g., Hutchison *et al.*, 1986; Hagstrum and Milliken, 1988). Temperature and RH influence popula-

tion trends of insect species by affecting developmental times, survival, and fecundity. Quantitative analyses of these environmental effects are important in understanding, predicting, and comparing population trends of insects living in the same or diverse habitats. Such models are also useful in predicting specific phenological events in the insect's life cycle, such as time of egg hatch, pupation, and adult emergence.

In this paper we used regression analyses to describe the development data of *P. truncatus* presented in Shires (1979) and Bell and Watters (1982). Our objectives were: (1) to fit models to temperature-dependent development data at each relative humidity; (2) to compare models to determine the influence of relative humidity on development; (3) to compare temperature-dependent development of *P. truncatus* reared on different diets (in compacted ground maize vs kernels of whole maize); (4) to compare development data of Shires (1979) with that of Bell and Watters (1982) at 70% or 80% RH; (5) to estimate temperatures for minimum and maximum developmental rates (1/developmental time) for various life-stages at each relative humidity, and the number of degree-days required for completing development; and (6) to provide methods for predicting insect development in the field under variable temperatures using the linear degree-day and the nonlinear development models. In addition, the egg, larval, and pupal development data given in Shires (1980) at 32°C and 80% RH were compared with similar data presented by Bell and Watters (1982).

2. Materials and methods

2.1. Fitting models to development data

The mean egg hatch to adult development data (Shires, 1979), and mean development of the egg, larval, and pupal stages (Bell and Watters, 1982) at each relative humidity level were described by the following four-parameter nonlinear regression model (Wagner *et al.*, 1984):

$$\text{Development time} = \frac{1 + \exp[HH/1.987(1/TH - 1/T)]}{RHO25(T/298.15) \exp[HA/1.987(1/298.15 - 1/T)} \quad (1)$$

where, $RHO25$ = development rate at 25°C (298.15 K), HA = enthalpy of activation of the reaction that is catalysed by a rate-controlling enzyme, HH = change in enthalpy associated with high-temperature inactivation of the enzyme, and TH = Kelvin temperature at which the rate-controlling enzyme is half active and half high-temperature inactive. Two other parameters, TL (Kelvin temperature at which the rate-controlling enzyme is half active and half low-temperature inactive) and HL (change in enthalpy associated with low temperature inactivation of the enzyme), were not included in equation (1) (see Wagner *et al.*, 1984), because there was limited or no data on the development of *P. truncatus* at temperatures below 18°C. Therefore, development data were described using the four-parameter model. Simpler regression models, such as a first-order polynomial, were not used to describe development, because Hagstrum and Milliken (1988) have shown that equation (1) best described the development of stored-product insects over a

range of temperatures compared with a polynomial model. Regression equations and values of parameters were generated by the Marquardt method of PROC NLIN procedure of the Statistical Analysis System (SAS Institute, 1987). The four-parameter model generally describes a backwards 'J'-shaped curve. Equation (1) was fitted to all of Shires (1979) data. The following data were excluded from Bell and Watters (1982) before fitting equation (1): data where development to adulthood was incomplete, data at 37°C where mortality was excessively high, and pupal development data at 18°C, 70% RH. The regressions were weighted with the number of survivors at each temperature. This weighting was necessary because the survival (Bell and Watters, 1982) or mortality (Shires, 1979) of *P. truncatus* varied at different temperatures.

2.2. Influence of relative humidity on development

Differences ($P < 0.05$) in development of the immature stages (Bell and Watters, 1982) or the egg hatch to adult development (Shires, 1979) between or among relative humidities were determined by comparison of individual regression models to a pooled model (Draper and Smith, 1981). Data were pooled where differences between models being compared were not significantly different from one another, and a model was fitted to the pooled data.

2.3. Influence of diet on development

Equation (1) was fitted to data on the mean egg to adult development of *P. truncatus* reared in tightly compacted ground maize and inside whole maize kernels at various temperatures and 70% RH (Bell and Watters, 1982). The development models on each diet were compared to a pooled model (Draper and Smith, 1981). Data were pooled if difference between the individual models was not significant ($P > 0.05$), and a model was fitted to the pooled data. However, Bell and Watters (1982) used the maize variety Golden Beauty for determining development in ground maize, and variety Spancross for determining development inside maize kernels. Therefore, varietal effects were verified before fitting equation (1), by comparing the egg to adult development data (Bell and Watters, 1982) of *P. truncatus* at 30°C and 70% RH inside whole kernels of varieties Golden Beauty and Spancross. A two-sample *t* test (two-tailed) for unequal variances (variance, s^2) was used (Snedecor and Cochran, 1980), because s^2 for development on Spancross variety was significantly greater than s^2 for development on Golden Beauty variety (*F*-test for equality of variances, $F = 2.01$; d.f. = 158,78; $P < 0.001$). Sample sizes were calculated from initial number of eggs used, and stage-specific mortality (see Bell and Watters, 1982). We assumed that the effect of variety on developmental times at temperatures other than 30°C was similar to the effect observed at 30°C.

2.4. Comparison between Shires (1979, 1980) and Bell and Watters (1982) data

Only the mean egg hatch to adult development data of *P. truncatus* at 70% or 80% RH could be compared between

Shires (1979) and Bell and Watters (1982), because temperature-dependent development data at these relative humidities were common to both studies. Equation (1) was fitted to Shires (1979) and Bell and Watters (1982) data at each relative humidity. At each relative humidity, differences ($P < 0.05$) between the studies were determined by comparing individual regression models to a pooled model (Draper and Smith, 1981).

Developmental times for the egg, larval, and pupal stages at 32°C and 80% RH given in Bell and Watters (1982) were compared with developmental times for similar life stages given in Shires (1980) using two-sample *t* tests (Snedecor and Cochran, 1980). A *t* test was not suitable for comparing the egg developmental time between the two studies, because s^2 was zero for data given by Bell and Watters (1982). Therefore, a 95% confidence interval (CI) was constructed for the mean egg developmental time based on Shires (1980) data, to determine if the egg developmental time reported by Bell and Watters (1982) was included within the CI. A *t* test for unequal s^2 ($F = 9.09$; d.f. = 112,20; $P < 0.001$) was used for comparing larval developmental time, whereas for comparing pupal developmental time a *t* test for equal s^2 ($F = 1.35$; d.f. = 112,20; $P = 0.224$) was used.

2.5. Estimating temperature thresholds and degree-days

The temperatures for maximum developmental rate (T_{max}) were estimated for the egg hatch to adult development at each relative humidity (Shires, 1979), egg to adult development in ground maize and inside whole maize kernels at 70% RH, and development of the egg, larval, and pupal stages at each relative humidity (Bell and Watters, 1982) using the nonlinear model of Stinner *et al.* (1974):

$$R_T = C/[1.0 + \exp(K1 + \{K2*T\})] \quad (2)$$

where R_T = rate of development at temperature T (in °C); C = maximum R_T ($1.0 + \exp(K1 + \{K2*T_{max}\})$); T_{max} = tem-

perature for maximum R_T ; $K1$, $K2$ = empirical constants, and $T' = T$ for $T \leq T_{max}$, or $T' = (2*T_{max}) - T$ for $T > T_{max}$. T_{max} , $K1$, $K2$, and C were estimated using the derivative-free (DUD) regression method (Ralston and Jennrich, 1978) of PROC NLIN procedure (SAS Institute, 1987).

The Stinner *et al.* (1974) model describes developmental rate as a function of temperature, and the response curve has a flattened 'S'-shaped appearance. The 'S'-shaped curve has three regions: at low temperatures the curve is an asymptote at rates near zero, a mid-region where the developmental rate increases linearly with temperature, and a region above the linear portion of the curve where the rates increase at a decreasing rate until T_{max} is reached. Beyond T_{max} the rates decrease rapidly. The Stinner *et al.* (1974) model incorrectly assumes that the developmental rates are symmetrical around T_{max} . The error in estimation of T_{max} induced by this assumption is negligible, because mortality of insects rapidly approaches 100% at temperatures above T_{max} (Stinner *et al.*, 1974).

The lower temperature threshold (T_{min}), where developmental rate is minimum (zero), and degree-days above T_{min} required for completion of the egg, larva, pupa, egg to adult (Bell and Watters, 1982), and egg hatch to adult development (Shires, 1979) were calculated (see Campbell *et al.*, 1974) by regressing developmental rates that were linearly related to the temperature using the PROC REG procedure (SAS Institute, 1987).

3. Results

3.1. Models describing development

The parameter values obtained using equation (1) for predicting the development of *P. truncatus* are presented in Table 1. A total of 19 equations were generated, but only 12 equations are presented because of pooling of data when models were not significantly different ($P > 0.05$) from one another. In general, developmental times for the egg, larval, and pupal stages (Figure 1), egg hatch to adult (Figure 2) or

Table 1. Parameters for equation describing the relationship between temperature and developmental time for *Prostephanus truncatus*, reared at different relative humidities in ground maize

Source of data	Stage	Relative humidity (%)	<i>n</i> ^a	RHO25	HA	HH	TH	<i>R</i> ²
Bell and Watters (1982)	Egg	40 + 70 + 80 + 90 ^b	23	0.476	37 581	36 903	295.1	0.966
		40	4	0.025	13 246	1 292 103	305.4	0.764
	Larva	70 + 80 ^b	13	0.319	86 538	85 898	294.4	0.994
		90	6	0.043	39 611	56 666	300.8	0.966
		40 + 70 + 80 + 90 ^b	22	0.423	46 544	44 164	294.7	0.969
	Pupa	40 + 70 + 80 + 90 ^b	22	0.423	46 544	44 164	294.7	0.969
		Egg hatch to adult	70	8	0.380	92 698	87 899	293.4
Egg to adult ^c	80	5	0.033	9 613	92 343	309.6	0.998	
	70	14	0.230	81 910	76 924	293.5	0.989	
Shires (1979)	Egg hatch to adult	50	6	0.021	27 513	67 014	304.8	0.998
		60	6	0.128	81 327	84 668	295.0	0.969
		70	6	0.024	19 883	75 174	306.6	0.999
		80	6	0.026	30 501	59 729	304.2	0.996

^a *n* = Number of observations used in fitting the development equation (equation 1).

^b Parameters of development equation estimated based on pooled data.

^c Analysis based on pooled data (insects reared in tightly compacted ground maize and inside whole maize kernels at 70% RH).

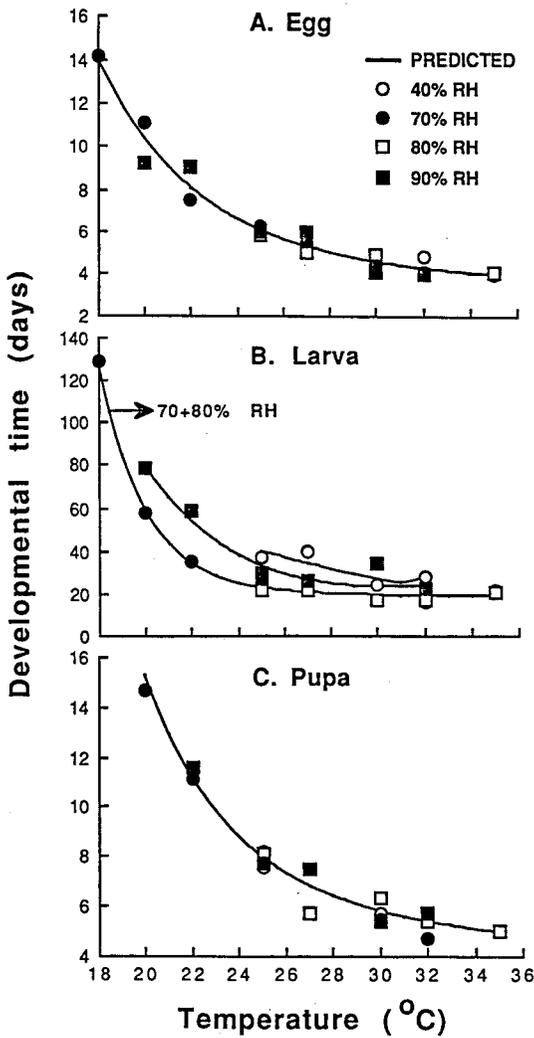


Figure 1. Observed and predicted mean developmental times for egg (A), larval (B), and pupal (C) stages of *Prostephanus truncatus* reared at constant temperatures and relative humidities (RH). A single predicted line (see Table 1) described the data where differences between or among relative humidities were not significant ($P > 0.05$).

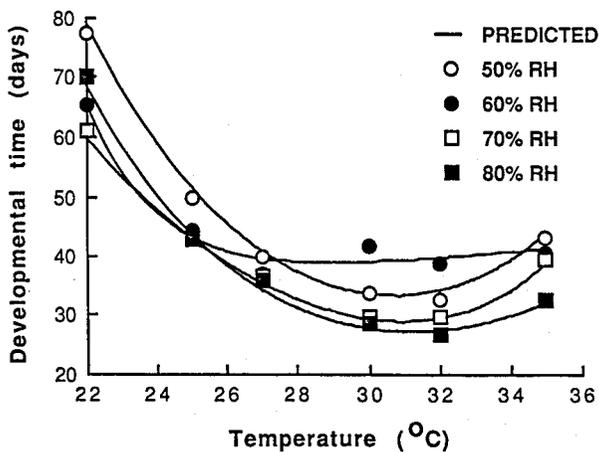


Figure 2. Observed and predicted mean egg hatch to adult developmental times for *Prostephanus truncatus* reared at constant temperatures and relative humidities (RH). Development among humidities was significantly different ($P < 0.05$).

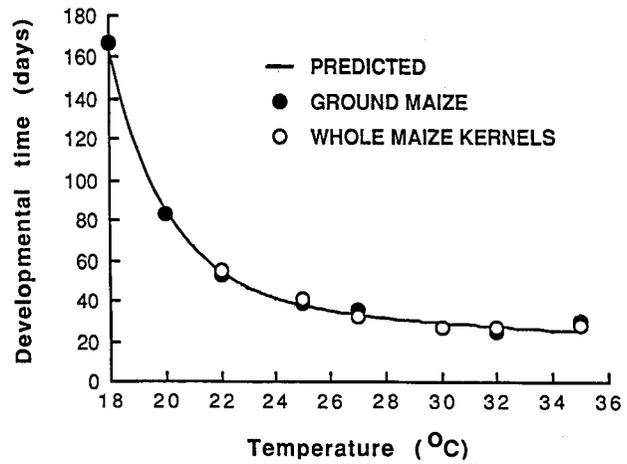


Figure 3. Observed and predicted mean egg to adult developmental times for *Prostephanus truncatus* reared in tightly compacted ground maize and inside whole maize kernels at 70% relative humidity (RH). Difference between the rearing diets in the developmental times was not significant ($P > 0.05$).

egg to adult development (Figure 3) decreased gradually with an increase in temperature. The egg hatch to adult developmental time (Figure 2) decreased until 31°C at 50%, 70%, and 80% RH, but increased at 35°C.

3.2. Influence of relative humidity on development

Comparison of development models indicated that the temperature-dependent development of eggs (Figure 1A) reared at 40%, 70%, 80%, and 90% RH was similar ($F = 0.60$; d.f. = 12,7; $P = 0.792$). The development of pupae (Figure 1C) was also not influenced by humidity ($F = 1.18$; d.f. = 10,8; $P = 0.415$). Humidity affected larval developmental time, and significant differences in larval development were detected among the humidities ($F = 3.66$; d.f. = 12,7; $P = 0.047$). However, the development of larvae (Figure 1B) reared at 70% and 80% RH was similar ($F = 0.66$; d.f. = 4,5; $P = 0.646$). The larval development at 70 + 80% RH was faster compared with development at 40% and 90% RH.

The egg hatch to adult development (Figure 2) between 70% and 80% RH was significantly different ($F = 11.86$; d.f. = 4,4; $P = 0.017$), and at temperatures $\geq 26^\circ\text{C}$ the development at 80% RH was faster compared with 70% RH. There were significant differences ($F = 11.00$; d.f. = 12,8; $P = 0.001$) in the egg hatch to adult development of *P. truncatus* among the humidities (50%, 60%, 70%, and 80% RH).

Predicted percentage of the total developmental time spent in each of the egg, larval, and pupal stages for *P. truncatus* over a range of temperatures (20–37°C) was similar at a given humidity level, but was different at 40%, 70 + 80%, and 90% RH (Table 2). Percentage of time spent among the three stages was as follows: larva > pupa > egg. Over a range of temperatures at 40% and 90% RH, percentage of time spent in the larval stage was longer, whereas time spent in the egg and pupal stages was shorter compared with similar data at 70 + 80% RH. Averaged across all humidities at 32°C, about 13%, 70%, and 17% of

Table 2. Predicted percentage of total developmental time spent in egg, larval, and pupal stages for *Prostephanus truncatus* reared in tightly compacted ground maize at different relative humidities

Relative humidity (%)	Percentage of development in stage ^a					
	Egg		Larval		Pupal	
	A	B	A	B	A	B
40	12	11-12	74	70-74	15	15-18
70 + 80	15	12-16	66	62-70	19	18-22
90	13	10-14	71	69-78	16	12-18
Mean	13		70		17	

^a For each stage the percentage at 32°C (A) and the range of percentages (B) over a range of temperatures (20, 22, 25, 27, 30 and 32°C at 40% RH; 20, 22, 25, 27, 30, 32, 35, and 37°C at 70 + 80, and 90% RH) were calculated using equation (1) and parameter values given in Table 1.

the total developmental time was spent in the egg, larval, and pupal stages, respectively.

3.3. Influence of diet on development

The egg to adult development at 30°C and 70% RH inside kernels of maize varieties Golden Beauty and Spancross was similar ($t = 1.41$; d.f. = 157; $P = 0.161$). Therefore, the egg to adult development at 70% RH in ground maize and inside whole maize kernels was compared, and there were no differences ($F = 2.42$; d.f. = 4,6; $P = 0.16$) in the development on these two diets (Figure 3).

3.4. Comparison between Shires (1979, 1980) and Bell and Watters (1982) data

The egg hatch to adult development data of Shires (1979) at all temperatures were significantly greater (i.e. development was slower) compared with Bell and Watters (1982) data at 70% RH (Figure 4A; $F = 29.74$; d.f. = 4,6; $P < 0.001$). Similar results were observed at 80% RH (Figure 4B; $F = 20.22$; d.f. = 4,3; $P = 0.017$). Observed differences in developmental time between the studies at 22-35°C and 70% RH ranged from 15.1 to 6.3 days, with greater differences associated with low and high temperatures. At 25-35°C and 80% RH, differences in developmental time between the studies ranged from 13.4 to 5.6 days.

Shires (1980) reported that at 32°C and 80% RH the average duration of the egg, larval, and pupal stages was 4.86, 25.40, and 5.16 days, respectively. Corresponding values from Bell and Watters (1982) were 4.00, 17.10, and 5.40 days, respectively. The 95% CI for the mean egg developmental time based on Shires (1980) data was ± 0.18 (lower limit 4.68 and upper limit 5.04), and this CI does not include the mean developmental time for the egg stage given by Bell and Watters (1982), indicating a slight, yet significant difference ($P < 0.05$) between the two studies. However, highly significant differences were observed in the larval developmental time between the studies ($t = 16.87$; d.f. = 80; $P < 0.001$). Shires (1980) data showed that larval development took 8.3 days longer compared with that of Bell

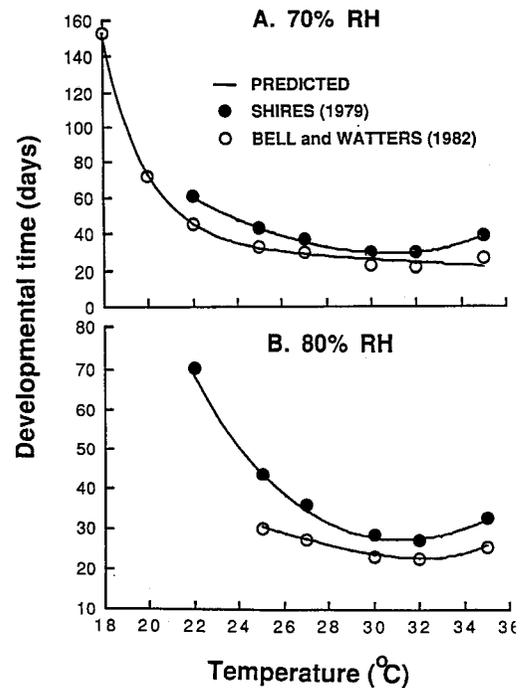


Figure 4. Comparison between Shires (1979) and Bell and Watters (1982) data in the mean egg hatch to adult developmental time for *Prostephanus truncatus* at 70% (A) and 80% (B) relative humidity (RH). Differences in development between the studies were significant ($P < 0.05$) at each humidity.

and Watters (1982). The pupal developmental times reported by Shires (1980) and Bell and Watters (1982) were similar ($t = 1.94$; d.f. = 132; $P = 0.055$).

3.5. Estimated temperature thresholds and degree-days

T_{max} for the development of the egg and pupal stages was 33°C and 34°C, respectively, while T_{max} for the larval development varied from 27°C to 31°C, depending on the relative humidity (Table 3). T_{max} for the egg to adult development in ground maize and inside whole maize kernels at 70% RH (Bell and Watters, 1982) was about 32°C. T_{max} for the egg hatch to adult development (Shires, 1979) was about 31°C at 50-80% RH.

T_{min} for development of the larval stage at 40%, 70 + 80%, and 90% RH was higher (15-17°C) than the egg (11°C) or pupal (13°C) stage (Table 4). T_{min} for the egg hatch to adult development at 50%, 70%, and 80% RH ranged from 12°C to 15°C. T_{min} at 60% RH could not be reliably estimated because the available data were anomalous (see Figure 2). The possible reasons for these anomalous data were fully discussed by Shires (1979).

About 84 and 99 degree-days were required for completing development of the egg and pupal stages, respectively (Table 4). The larval stage required 2.6- to 4.1-fold more degree-days at 40%, 70 + 80%, and 90% RH to complete development compared with the egg and pupal stages. Degree-days required for completion of the egg hatch to adult development at 50%, 70%, and 80% RH ranged from 435 to 556. However, degree-days required for the egg hatch to adult development at 60% RH were two times

Table 3. Parameters (mean \pm SE) for Stinner et al. (1974) model describing the temperature-dependent development of *Prostephanus truncatus* at different relative humidities

Source/stage	n^a	T_{max}	K1	K2	C	R^2
Bell and Watters (1982)						
Egg (pooled)	25	33.41 \pm 0.59	4.61 \pm 0.74	-0.20 \pm 0.04	0.28 \pm 0.03	0.939
Larva						
40% RH	4	30.68 \pm 1.23	4.37 \pm 3.63	-0.12 \pm 0.24	0.13 \pm 0.00	0.829
70 + 80% RH	13	31.01 \pm 0.30	6.41 \pm 0.96	-0.27 \pm 0.05	0.07 \pm 0.01	0.965
90% RH	5	27.15 \pm 0.49	8.78 \pm 3.68	-0.38 \pm 0.19	0.05 \pm 0.01	0.981
Pupa (pooled)	23	34.09 \pm 1.98	5.46 \pm 2.51	-0.23 \pm 0.12	0.22 \pm 0.05	0.915
Egg to adult ^b	14	31.67 \pm 0.90	6.14 \pm 0.62	-0.26 \pm 0.03	0.04 \pm 0.003	0.985
Shires (1979)						
Egg hatch to adult						
50% RH	6	30.84 \pm 0.23	6.14 \pm 1.22	-0.25 \pm 0.06	0.04 \pm 0.006	0.991
60% RH	6	30.66 \pm 1.81	14.10 \pm 8.76	-0.66 \pm 0.40	0.03 \pm 0.002	0.915
70% RH	6	30.73 \pm 0.19	4.47 \pm 0.76	-0.16 \pm 0.05	0.06 \pm 0.02	0.993
80% RH	6	31.50 \pm 0.11	6.29 \pm 0.47	-0.25 \pm 0.02	0.04 \pm 0.002	0.999

^a n = Number of observations used in fitting the model.

^b Analysis based on pooled data (insects reared in tightly compacted ground maize and inside whole maize kernels at 70% RH).

greater than degree-days required for the same development at other humidities.

4. Discussion

Developmental times for the various life stages of *P. truncatus* at different temperatures and humidities, or on different diets, were best described by the four parameter regression model (equation 1), with R^2 in most cases being ≥ 0.966 .

Relative humidity influenced developmental times by affecting only the larval development; humidity did not affect development of the eggs and pupae. Relative humidity may have directly affected the metabolism (e.g. respiration) of actively feeding larvae, or may have indirectly influenced

larval feeding by affecting the palatability or physical condition of the rearing diet (ground maize).

Percentages of total developmental time spent in the egg, larval, and pupal stages at various temperatures reported for *P. truncatus* are comparable to percentages reported for six other stored-grain insect species (Hagstrum and Milliken, 1988). The number of individuals in a given stage is proportional to the developmental time of that stage when the population reaches a stable age distribution (Hagstrum, 1991). Therefore, these constant percentages of the total developmental time for a particular stage at different temperatures indicate that the number of insects in that stage at stable age distribution will be the same over the range of temperatures reported. A change in the percentage of the total developmental time of each stage with relative humidity suggests that the number of individuals in that

Table 4. Estimates (mean \pm SE) of temperature for minimum developmental rate (T_{min}) and degree-days (DD) above T_{min} required for completion of development of *Prostephanus truncatus* at different relative humidities

Source/stage	n	T_{min}	DD $>$ T_{min}	R^2	Temperature ($^{\circ}$ C) ^b
Bell and Watters (1982)					
Egg (pooled)	21	11.36 \pm 0.88	84.23 \pm 4.65	0.945	18-35
Larva					
40% RH	3	16.65 \pm 5.93	346.74 \pm 189.42	0.771	25-30
70 + 80% RH	11	14.61 \pm 0.91	273.67 \pm 19.99	0.954	18-32
90% RH	4	16.97 \pm 0.90	259.47 \pm 32.97	0.969	20-27
Pupa (pooled)	21	13.05 \pm 0.94	98.81 \pm 6.45	0.925	18-35
Egg to adult ^c	10	15.05 \pm 0.38	403.88 \pm 14.83	0.989	18-30
Shires (1979)					
Egg hatch to adult					
50% RH	5	14.24 \pm 1.51	548.25 \pm 61.96	0.963	22-32
60% RH	4	3.40 \pm 7.70	1091.70 \pm 347.64	0.831	22-32
70% RH	5	12.31 \pm 1.79	555.86 \pm 65.11	0.961	22-32
80% RH	5	15.29 \pm 0.95	435.35 \pm 33.21	0.983	22-32

^a n = Number of observations used in the linear regression.

^b Developmental rates were linear over these temperature ranges.

^c Analysis based on pooled data (insects reared in tightly compacted ground maize and inside whole maize kernels at 70% RH).

stage when population reaches stable age distribution will be different at different humidities.

There were no differences in the egg to adult development of *P. truncatus* reared in tightly compacted ground maize and inside kernels of whole maize. This suggested that tightly compacted ground maize provides an environment similar to that experienced by insects developing inside whole maize kernels. Compaction of loose whole maize kernels also facilitates adult tunnelling activities (Howard, 1984), because tightly compacted kernels are relatively stable for effective boring by adults (Cowley *et al.*, 1980). In addition, flour produced by adults of *P. truncatus* is such tightly compacted shelled grain provides an ideal medium for larval survival and development (Bell and Watters, 1982).

The observed differences in the egg hatch to adult development between Shires (1979) and Bell and Watters (1982) data were noteworthy. Comparison of individual life stages between the studies at 32°C and 80% RH indicated that these differences were caused mainly by differences in the larval development. Shires (1979, 1980) did not tightly compact ground maize in his experiments. Bell and Watters (1982), using loosely and tightly compacted ground maize at 30°C and 70% RH, showed that tight compaction was necessary for normal development and survival. At 32°C and 70% RH, the difference in the egg to adult development period between loosely and tightly compacted ground maize was 6.3 days (Bell and Watters, 1982). The egg hatch to adult development period differences between Shires (1979) and Bell and Watters (1982) at 22–35°C and 70% RH ranged from 15.1 to 6.3 days. In addition, these differences do not include the egg development period, which is about 7.5–4 days at 22–35°C. Therefore, differences between the studies in development cannot be entirely attributed to differences in the degree of ground maize compaction. The strain of *P. truncatus* used by Shires (1979) was obtained from Nicaragua, while the strain used by Bell and Watters (1982) was obtained from Mexico. Variation in larval development between the strains may have contributed to the differences observed between the studies.

T_{max} and T_{min} varied with the insect stage and relative humidity. T_{max} calculated for the egg and pupal stages was 2–7°C higher compared with the larval stage. Shires (1979) and Bell and Watters (1982) reported that 32°C was the optimum temperature for the egg hatch to adult and egg to adult development of *P. truncatus*, respectively. Our estimated T_{max} for the egg to adult development based on Bell and Watters (1982) data was 31.67°C, whereas T_{max} for the egg hatch to adult development was 0.5–1.0°C lower than that reported by Shires (1979). T_{min} estimates are essential for accumulating degree-days to predict *P. truncatus* development in the field (Higley *et al.*, 1986). Inclusion of T_{max} in degree-day calculations may improve the accuracy of estimates (Higley *et al.*, 1986), because mortality of insects approaches 100% as temperatures increase beyond T_{max} (Stinner *et al.*, 1974). Higley *et al.* (1986) have discussed assumptions and limitations of the degree-day approach, and they also provided simple and complex methods for computing degree-days using ambient (or in our case, grain) temperatures. For example, degree-day for a given day (DD'') is calculated as the difference between the average

daily temperature (T_i ; calculated from temperatures recorded hourly or from daily minimum and maximum temperatures) and T_{min} . DD'' are computed by summing $(T_i - T_{min})$ over successive increments of time (Δt) as

$$DD'' = \sum (T_i - T_{min}) * \Delta t \quad (3)$$

where Δt is a day ($t = 1$), half-day ($t = 0.5$), or an hour ($t = 0.042$). Development is assumed to be completed when DD'' is equal to or exceeds the degree-days estimated from constant temperature-development rate experiments (see Table 4). T_{max} is included in DD'' calculations only if T_i exceeds T_{max} ; i.e. substitute T_{max} for T_i in equation (3). The degree-day approach is simple but suitable only if temperatures in *P. truncatus*-infested areas fall within the linear portion of the curve. If temperatures in the field fall outside the linear portion of the curve, *P. truncatus* development can be predicted using an inverted equation (1). Equation (1) is inverted to predict developmental rate or the proportion of temperature-dependent development of an insect stage that is completed for each time increment. Development is predicted by measuring T_i as explained above, and the rate of development for that day (or smaller increments of time) is determined using an inverted equation (1). In the inverted equation (1), T is replaced with T_i (in Kelvin); the remaining four-parameter values are obtained from Table 1. Development of an average insect stage or stages is assumed completed when the accumulated rates are ≥ 1 . The data of Bell and Watters (1982) should be used for predicting *P. truncatus* development, because Shires (1979) data do not include the egg development period, and larval development was not 'normal' as a result of rearing insects in loosely compacted ground maize. However, the accuracy with which the temperature thresholds, degree-days, and the nonlinear model estimates could be used in the field for predicting *P. truncatus* development has not been tested.

In the future, population trends of *P. truncatus* can be predicted using the development models presented here in conjunction with age-specific fecundity and adult longevity data, also collected at various temperatures and relative humidities (e.g. Hagstrum and Throne, 1989). Shires (1980) studied adult longevity and fecundity of *P. truncatus* at 32°C and 80% RH, and Bell and Watters (1982) presented fecundity and longevity data at two temperatures (30° and 32°C) and relative humidities (70% and 80% RH). However, these data are too limited for simulating population trends using the information presented in this paper. Predicting development and population trends of *P. truncatus* in the field will be valuable for determining the optimum time for sampling insects and scheduling control tactics.

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