

A comparison of the demography of four major stored grain coleopteran pest species and its implications for pest management

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Abstract

Detailed demographic data are now available for four of the major stored grain pests, *Sitophilus oryzae*, *Rhyzopertha dominica*, *Oryzaephilus surinamensis* and *Tribolium castaneum*, over a comprehensive range of temperature and relative humidity combinations.

This paper presents a between species comparison of the major demographic components of age specific survival and fertility, immature development period and finite rate of increase. The variation between species, evident in the data, is reflected in their environmental limits, as well as in the optimum and suboptimum conditions for reproduction and population growth.

The implications of these findings for pest management, especially with regard to setting limits for grain receival moisture content and for aeration strategies, are discussed.

Introduction

In Australia, the current status of four of the major stored grain coleopteran pest species, *Sitophilus oryzae*, *Rhyzopertha dominica*, *Oryzaephilus surinamensis* and *Tribolium castaneum*, is in part a reflection of the changing history of pest management practices this century.

Prior to the introduction of malathion between 1960 and 1965 (Murray 1979), *S. oryzae* was a major problem in Australia. The insect caused significant storage losses and was frequently identified in grain exports. From 1917 to 1919, for example, numerous outbreaks in Victoria, South Australia and New South Wales reached what were considered to be plague proportions (Winterbottom 1922). However, with the systematic application of malathion, a dramatic decline in the incidence of the pest occurred. Since then, the low levels achieved have been maintained with new generations of pesticides and, in general, it now ranks a poor fourth in the frequency of reported infestations at central storages (Bulk Grains Queensland Ltd (BGQ) 1991; Co-operative Bulk Handling Western Australia Ltd (CBH WA) 1991; Grain Elevators Board of Victoria (GEB Vic.) 1991; NSW Grain Corporation Ltd (GrainCorp) 1991; South Australian Co-operative Bulk Handling Ltd (SA-CBH) 1991).

R. dominica, on the other hand, has consistently been a major stored grain pest. It was the repeated occurrence of malathion resistant strains of *R. dominica*, rather than *S. oryzae*, that led to the urgent development of alternative pesticides in the 1970s (Murray 1979). The majority of phosphine-resistant strains reported so far have also been *R. dominica* (Caddick 1990). Today, it is consistently the most frequent

cause of infestations at central storages and rejections at point of export (BGQ 1991; CBH WA 1991; GEB Vic. 1991; GrainCorp 1991; SA-CBH 1991; Australian Wheat Board (AWB) 1988).

Traditionally, *O. surinamensis* and *T. castaneum* have not been considered major threats to grain exports in Australia. In the past, outbreaks of *O. surinamensis* have been relatively uncommon. However, over the past decade, the incidence of this insect has increased significantly (BGQ 1991; CBH WA 1991; GEB Vic. 1991; GrainCorp 1991; SA-CBH 1991; AWB 1988). It is now a key pest in some areas and is becoming a threat to grain exports. A major contributing factor appears to have been the development of pesticide resistance (Allen et al. 1988; insect resistance to grain protectants in the Victorian central grain handling system 1988; Sproul and Emery 1988; Wallbank 1988).

On the other hand, the reported incidence of *T. castaneum* has generally been consistent and though it has been relatively easy to treat, outbreaks of this pest have been quite frequent. For this reason, the cost of control makes it economically important (BGQ 1991; CBH WA 1991; GEB Vic. 1991; GrainCorp 1991; SA-CBH 1991; AWB 1988).

Experience has shown that significant changes in pest management or grain storage have the potential of altering the relative status of stored grain pests. The decline in importance of *S. oryzae*, for example, coincided with the conversion from bag to bulk storage in the 1950s and, as previously mentioned, the introduction of residual chemical protectants in the 1960s. Today, pest management relies less on the application of protectants and more on alternatives such as phosphine fumigation and aeration. If *S. oryzae*, which already is relatively tolerant to phosphine, were to develop major resistance to that fumigant, it has the potential to become a serious pest once again. The general move away from the residual treatment of grain, as well as higher receival limits for grain moisture at central storages, could further compound the problem.

To understand the extent of a potential problem, such as the one outlined above, it is essential to have detailed demographic data of the major pest species over a comprehensive range of temperature and moisture combinations. With such information, predictions can be made as to the potential threat of a given mixed infestation in a defined environmental condition and the likely dominant species. Furthermore, by knowing those conditions close to the theoretical development and the theoretical population growth thresholds for each species, steps can be taken which will avoid a major infestation of one or more of these species.

Detailed demographic data are now available for four major pest species on wheat, over a comprehensive range of temperature and relative humidity combinations (Longstaff, unpublished data; Beckett and Evans 1994; White 1987; Longstaff and Evans 1983), enabling a comparison to be made of the effects of environment on the population growth of each species. This paper reviews the data for the main demographic parameters and represents them in a directly comparable format. It discusses the population dynamics of each species

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and explores the possible implications for pest management in the light of the different demographics exhibited.

The Demographic Data

The range of available demographic data varies for each species. Data for *S. oryzae* exist at temperatures from 15 to 32.5°C and at relative humidities from 20% to 70% r.h. (Longstaff and Evans 1983); data for *R. dominica* exist from 15 to 39°C for the same range of relative humidities (Longstaff, unpublished data); data for *O. surinamensis* range from 20 to 35°C and from 30 to 70% r.h. (Beckett and Evans 1994); and finally, data for *T. castaneum* generally cover a range from 20 to 40°C and from 35 to 70% r.h. (White 1987). Although these four studies were carried out under broadly similar environmental conditions, specific temperature and relative humidity combinations often differ between them. Therefore, it has frequently been necessary to interpolate between points so that a direct comparison can be made.

The effect of temperature on a given demographic parameter has been considered over the full range of available data for each species. On the other hand, consideration of the effect of relative humidity has been limited to four equally spaced conditions over the best range for direct comparison. These are 35%, 45%, 55%, and 65% r.h. For *S. oryzae*, it was necessary to convert measurements of percentage moisture content to the equivalent relative humidity (Wilson 1990).

The data for *S. oryzae*, *R. dominica* and *O. surinamensis* have been gained for optimum rearing conditions. Both *S. oryzae* and *R. dominica* were reared on whole wheat (var. Olympic), while *O. surinamensis* was reared on kibbled wheat (var. Corella). On the other hand, *T. castaneum* was reared on partly broken whole wheat (var. Oxley), which though not optimum for population growth, reflects a realistic grain storage environment for the insect (White 1987). All four species were reared in a pesticide-free environment.

The description of the rate of population growth has been standardised in terms of the weekly finite rate of increase (λ) (Birch 1948), which is the natural antilog of the weekly infinite rate of increase (r_m). Actual and interpolated data are used for all species, except in the case of *T. castaneum*, where all data are interpolated from a three dimensional graph (White 1987).

To gain information on the possible variation in demographic strategy employed by the four species, data for the net rate of reproduction (R_0) and adult survival (l_x) have been compared after an 8-week period. Eight weeks was chosen as the maximum observation period common to all species and conditions. As 95% of the value of λ at a given condition is accounted for by the time parental females reach an age equivalent to their immature development period (Birch 1948, Figure 3), the presented values of R_0 are close to those required to achieve the actual values of λ , at temperatures roughly above 21°C for *S. oryzae* and *O. surinamensis*, and 24°C for *R. dominica* and *T. castaneum*. The value of R_0 depends on the product of a female's fertility and her ability to survive. By considering adult survival, an indication of its impact on the net rate of reproduction can be determined.

Furthermore, the relative combined effects that differences in the net rate of reproduction and the immature development period (D) have on the value of λ have also been considered. The relationship can be described in simple terms by the expression $r_m = \log_e R_0/T_c$, where T_c (the cohort generation time) is the sum of the mean age of the female at oviposition and the immature development period (Evans 1982). Where models have been developed to describe fertility and

survival, as in the case of *S. oryzae* and *T. castaneum*, these have been used to extract the required data.

The relationship between the weekly finite rate of increase (λ), temperature and relative humidity for all species is displayed in Figure 1. In general, the rate of population growth increases as temperature increases at a given relative humidity until an optimum temperature is reached. That temperature and the maximum population growth rate achieved differ for each species. In all situations, populations subjected to drier conditions grow slower than those subjected to more moist conditions. Above the optimum temperature for population growth, the rate of growth declines rapidly.

However, at 35% r.h. values of λ for *S. oryzae* are below 1 and decline with increasing temperature, indicating negative population growth. In the case of *T. castaneum*, White (1987) was unable to observe immature development at temperatures at 35% r.h. However, this model predicts a very small positive population growth between 25 and 35°C ($\lambda = 1.01$ to 1.11). Because of this discrepancy, values of λ at 35% r.h. have not been considered in this study. On the other hand, under similar circumstances positive population growth rates start to increase at 19 and 20°C for *R. dominica* and *O. surinamensis*, with a maximum value of λ (1.63) achieved by *R. dominica* at 30 and 33°C, and by *O. surinamensis* (1.78) at 30°C. Rates of growth for both species are similar as temperature increases to 24°C. Then, from 25 to 32°C the dry conditions favour *O. surinamensis* more so than *R. dominica*. However, as temperature increases further the population growth rate for *O. surinamensis* quickly decreases and reaches zero ($\lambda = 1$) by 35°C. The value of λ for *R. dominica* starts to decrease at about the same temperature but not as rapidly, with a λ value of 1 being reached between 37 and 38°C.

The general relationship of initial increase in population growth rate with increased temperature occurs for *S. oryzae* at the higher relative humidities considered (45%, 55%, and 65% r.h.), with maximum values of λ (1.77, 1.93, and 2.03) achieved at 27°C. For the other species, maximum values of λ (1.94, 2.21, and 2.39) are achieved by *R. dominica* at 33°C, *O. surinamensis* (1.95, 2.13, and 2.29) at 32°C, and *T. castaneum* (1.64, 2.05, and 2.31) at 35°C.

As temperature increases to 27°C at the higher relative humidities, the value of λ for *S. oryzae* is consistently greater than that for the other species. However, at 30°C at 45% r.h. the value of λ is less than that for *R. dominica* and *O. surinamensis*, and at 30°C at 55% and 65% r.h. it is also less than that for *T. castaneum*. On the other hand, as temperature increases to 32.5°C at these relative humidities, λ values for *R. dominica* and *O. surinamensis* are similar. Above this temperature, the population growth rate for *O. surinamensis* decreases faster than that for *R. dominica*. By contrast, values of λ for *T. castaneum* are the lowest for all species over the majority of temperatures/humidity combinations. However, in general, the relative difference in the size of the value of λ at a given temperature decreases as relative humidity increases so that the rate of population growth at a given temperature at 65% r.h. is very similar to that for *R. dominica* and *O. surinamensis*. Moreover, *T. castaneum* reaches its optimum population growth rate at a higher temperature (35°C) at relative humidities above 35% r.h. than all other species. At 37°C, λ values for *T. castaneum* at these relative humidities are greater than those for *R. dominica* and it is still achieving positive population growth rates at 39°C/55% r.h. and 40°C/65% r.h.

Since initially the relationship between the rate of population growth and temperature for a given relative humidity is more or less linear, theoretical thresholds of population growth have been calculated for the four species (Table 1). Apart from negative population growth for *S. oryzae* at temperatures at 35% r.h., the thresholds of population growth are

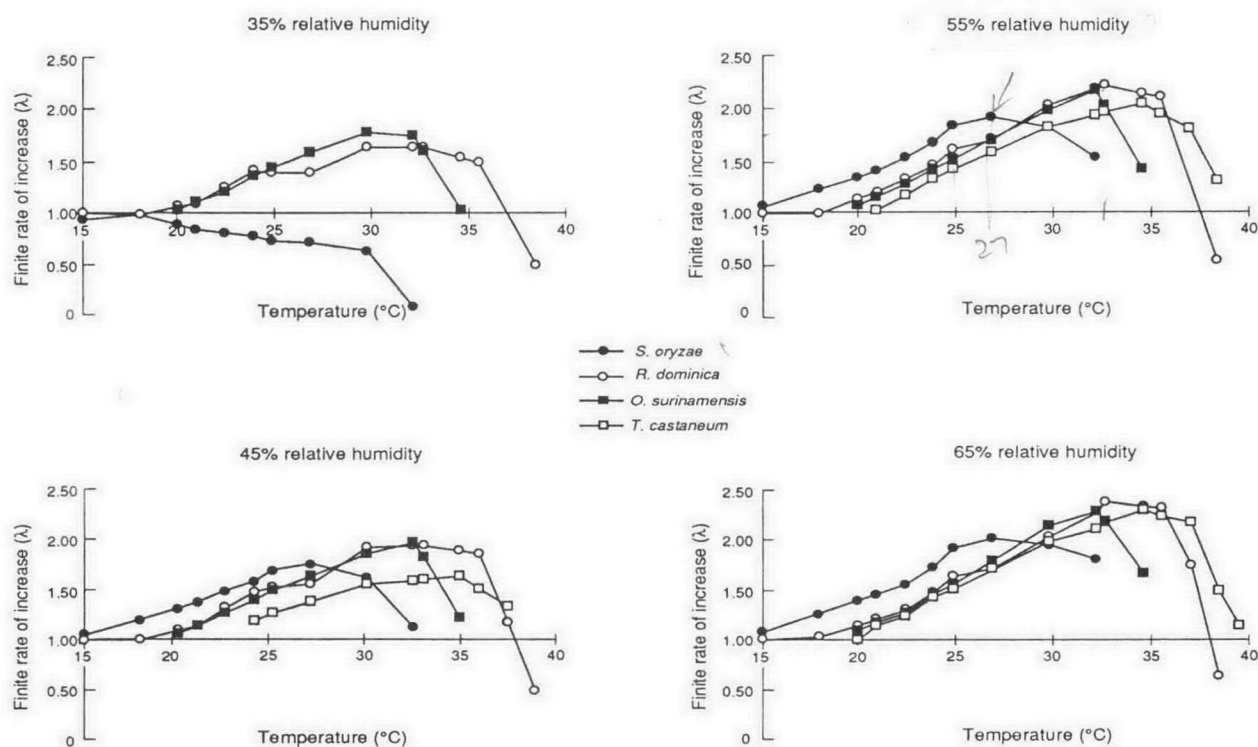


Fig. 1. The weekly finite rate of population increase (λ) for four stored-grain coleopteran species over a range of temperature ($^{\circ}\text{C}$) and relative humidity (r.h.) combinations.

Table 1. The threshold of weekly finite rate of reproduction (λ) for four stored-grain coleopteran species in terms of wet bulb (T_{wb}) and dry bulb (T_{db}) temperature ($^{\circ}\text{C}$) over a range of relative humidities (r.h.).

% r.h.	T_{wb} ($^{\circ}\text{C}$)	r^2	T_{db} ($^{\circ}\text{C}$)	r^2	n	T_{wb} ($^{\circ}\text{C}$)	r^2	T_{db} ($^{\circ}\text{C}$)	r^2	n
<i>Sitophilus oryzae</i>					<i>Rhyzopertha dominica</i>					
35.0	-	-	-	-	-	9.3	0.9274	17.3	0.9287	11
45.0	8.8	0.9892	14.7	0.9905	8	10.9	0.9532	17.4	0.9545	11
55.0	10.2	0.9778	14.9	0.9785	8	12.3	0.9722	17.5	0.9728	11
65.0	11.2	0.9766	14.8	0.9782	8	13.8	0.9659	17.7	0.9652	11
<i>Oryzaephilus surinamensis</i>					<i>Tribolium castaneum</i>					
35.0	11.0	0.9959	19.3	0.9963	7	-	-	-	-	-
45.0	12.1	0.9911	18.9	0.9920	8	13.5	0.9946	20.7	0.9970	4
55.0	13.6	0.9989	19.1	0.9989	8	14.7	0.9958	20.3	0.9969	6
65.0	15.2	0.9978	19.3	0.9975	8	15.5	0.9969	19.8	0.9974	7

little affected by the different relative humidities considered (*S. oryzae*: 14.8 $^{\circ}\text{C}$, SD 0.08; *R. dominica*: 17.5 $^{\circ}\text{C}$, SD 0.15; *O. surinamensis*: 19.2 $^{\circ}\text{C}$, SD 0.17; *T. castaneum*: 20.3 $^{\circ}\text{C}$, SD 0.37).

Values of R_0 for each species, i.e. the sum of adult female progeny per original female over an 8-week period, are displayed in Figure 2. The relationship between R_0 , temperature and relative humidity, is similar to that of λ with values increasing as temperature increases until an optimum is reached. Beyond this optimum the values for R_0 quickly decrease. Values at a given temperature are also generally lower at drier conditions than at more moist conditions. Maximum values at temperatures ranging from dry to moist

conditions range from 74.6 at 24 $^{\circ}\text{C}$ /45% r.h. to 131.7 at 24 $^{\circ}\text{C}$ /65% r.h. for *S. oryzae*, 158.2 at 24 $^{\circ}\text{C}$ / 35% r.h. to 316.9 at 35 $^{\circ}\text{C}$ /65% r.h. for *R. dominica*, 41.5 at 30 $^{\circ}\text{C}$ /35% r.h. to 117.0 at 32.5 $^{\circ}\text{C}$ /65% r.h. for *O. surinamensis*, and 3.5 at 30 $^{\circ}\text{C}$ /35% r.h. to 245.1 at 35 $^{\circ}\text{C}$ / 65% r.h. for *T. castaneum* (values for R_0 at 35% r.h. for *T. castaneum* are predicted rather than actual).

In general, after an 8-week period, as temperature increases at 35% r.h., adult survival (L_x) starts to decrease below 80% at 24 $^{\circ}\text{C}$ for *S. oryzae*, 30 $^{\circ}\text{C}$ for *R. dominica*, 35 $^{\circ}\text{C}$ for *O. surinamensis* and 32 $^{\circ}\text{C}$ for *T. castaneum*. However, over the range of temperatures up to 33 $^{\circ}\text{C}$ at relative humidities above 35% r.h., survival for all species, apart from *O. surinamensis*, is not less

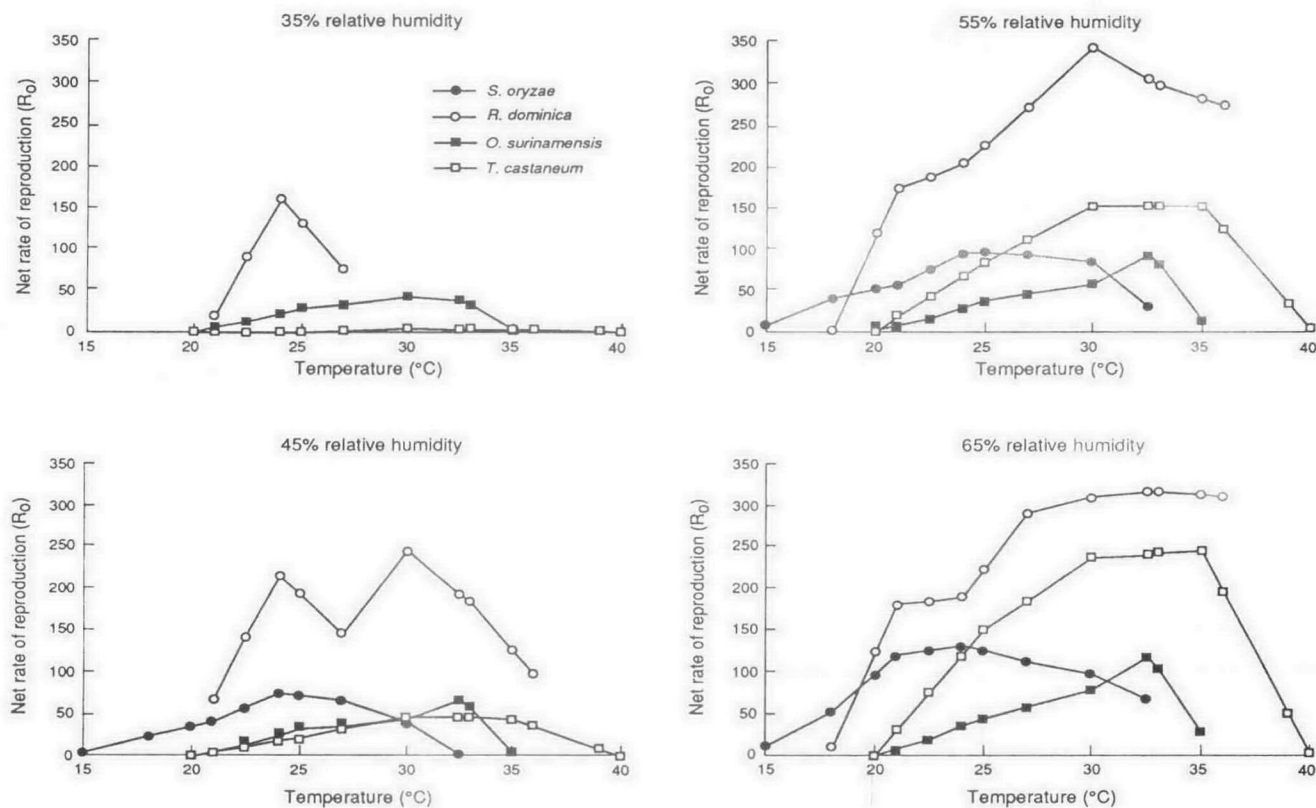


Fig. 2. The net rate of reproduction (R_0) after an 8-week period, for four stored grain coleopteran species over a range of temperatures ($^{\circ}\text{C}$) and relative humidity (r.h.) combinations.

than 80%. Survival for *O. surinamensis* on the other hand drops slightly between 24 and 30 $^{\circ}\text{C}$ at 35% r.h. and 27 and 30 $^{\circ}\text{C}$ at 45% and 55% r.h., but remains above 65%. Values of l_x are not available above 33 $^{\circ}\text{C}$ for *S. oryzae*, but are available for *R. dominica* up to 39 $^{\circ}\text{C}$. Therefore, it can be seen that values of l_x for *R. dominica* only drop below 60% at 35 $^{\circ}\text{C}/35\%$ r.h. and 39 $^{\circ}\text{C}$ at the higher relative humidities. At these latter conditions adult mortality suddenly becomes more or less complete. Data are not available for *O. surinamensis* above 35 $^{\circ}\text{C}$, but survival is not less than 50% at this temperature at 35% r.h. and not less than 60% at the higher relative humidities. Values of l_x for *T. castaneum* decrease rapidly at 35 $^{\circ}\text{C}/35\%$ r.h. and at 39 $^{\circ}\text{C}$ at the higher relative humidities. However, at 39 $^{\circ}\text{C}$, survival is still between 10 and 25%, but mortality more or less complete at 40 $^{\circ}\text{C}$. Therefore, for most conditions, there are high levels of adult survival for all species after 8 weeks, suggesting relatively similar limited effects on the final values of R_0 . Low survival after 8 weeks, which has a major impact on the value of R_0 , is only apparent at very suboptimum conditions specific for each species.

The data for immature development (D) are displayed in terms of a rate, $1/D$, in Figure 3. Like values of λ and R_0 there is a similar relationship between development period, temperature and relative humidity, with development periods becoming increasingly shorter as temperature increases, until an optimum is reached. Furthermore, development periods are longer at drier conditions than at more moist conditions. At all temperatures at 35% r.h. both *S. oryzae* and *T. castaneum* are unable to develop. However, for *R. dominica* the optimum development temperature at 35% r.h. is 33 $^{\circ}\text{C}$ (42.3D) and for *O. surinamensis* it is 32.5 $^{\circ}\text{C}$ (25.2D). The optimum development temperature for *S. oryzae* is 30 $^{\circ}\text{C}$ at the higher relative

humidities (42.0, 38.5, and 35.7D), for *R. dominica* it is 33 $^{\circ}\text{C}$ (33.7, 30.3, and 29.2D), for *O. surinamensis* they are 32.5 $^{\circ}\text{C}$ at 45% and 55% r.h., and 35 $^{\circ}\text{C}$ at 65% r.h. (23.7, 22.5, and 21.4D), and for *T. castaneum* it is 35 $^{\circ}\text{C}$ (30.6, 25.4, and 22.3D).

Values for $1/D$ have also been used to determine the theoretical development thresholds and thermal constants for each species at the four relative humidities (Table 2). Apart from the inability of *S. oryzae* and *T. castaneum* to develop at 35% r.h., the theoretical development thresholds for each species are little affected by the difference in the relative humidities considered (*S. oryzae*: 11.4 $^{\circ}\text{C}$, SD 0.27; *R. dominica*: 16.6 $^{\circ}\text{C}$, SD 0.52; *O. surinamensis*: 15.3 $^{\circ}\text{C}$, SD 0.27; *T. castaneum*: 16.8 $^{\circ}\text{C}$, SD 0.44). On the other hand, thermal constants range from 703 day degrees at 45% r.h. to 609 at 65% r.h. for *S. oryzae*, 730 day degrees at 35% r.h. to 483 at 65% r.h. for *R. dominica*, 393 day degrees at 35% r.h. to 327 at 65% r.h. for *O. surinamensis*, and 548 day degrees at 45% r.h. to 372 at 65% r.h. for *T. castaneum*.

Discussion

Species differ in the range of environmental conditions at which they show positive population growth and in those conditions at which population growth is at an optimum.

In general, the demography of *S. oryzae* is unsuited to higher temperatures at lower humidities, but is favoured above the other species at cooler more moist conditions. On the other hand, *R. dominica* thrives more so than any other species over the greatest range of temperature and relative humidity combinations. This is especially true at higher temperatures over all

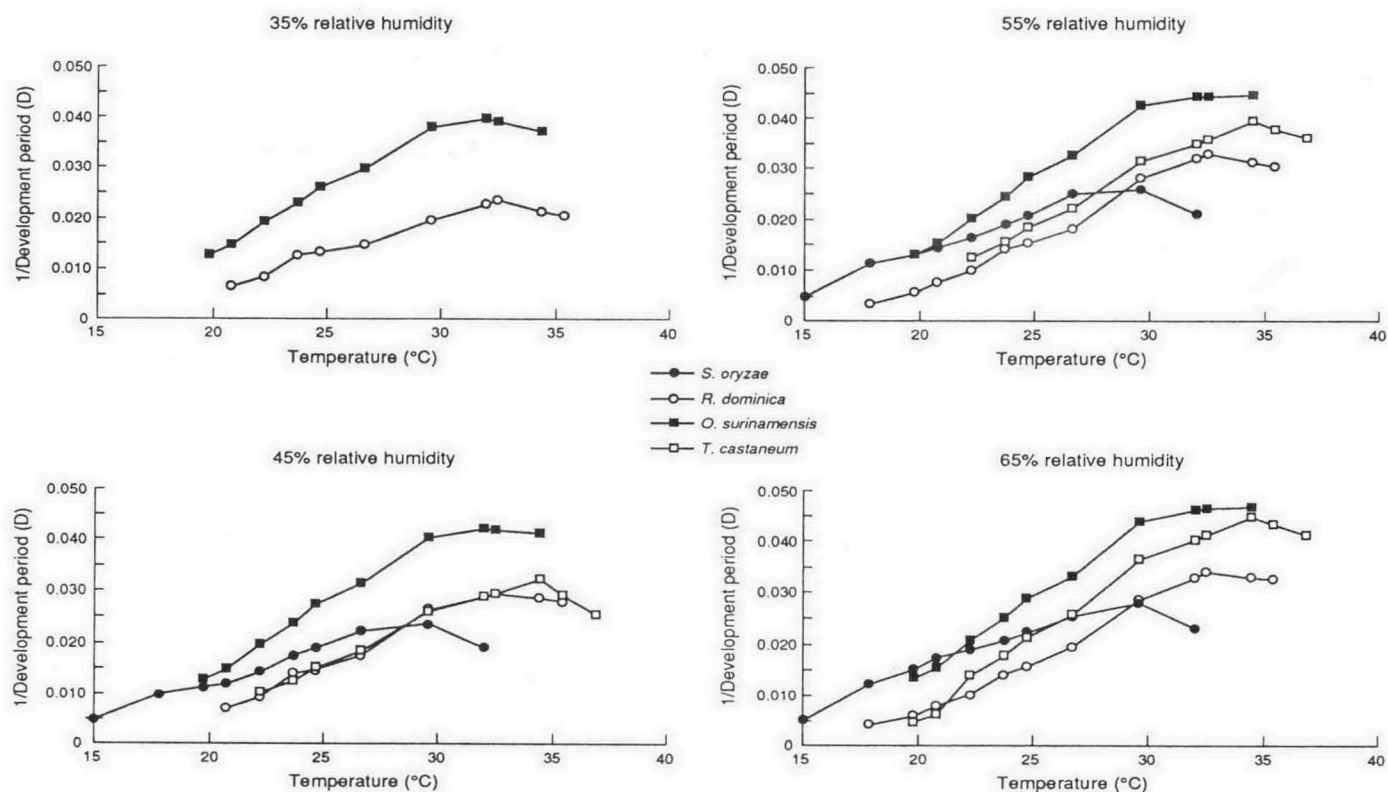


Fig. 3. The net rate of immature development ($1/D$) for four stored grain coleopteran species over a range of temperature ($^{\circ}\text{C}$) and relative humidity (r.h.) combinations.

Table 2. The theoretical development thresholds ($^{\circ}\text{C}$) and thermal constants (day degrees) for four stored-grain coleopteran species over a range of relative humidities (r.h.)

% r.h.	Development threshold	Thermal constant	r^2	Development threshold	Thermal constant	r^2
	<i>Sitophilus oryzae</i>			<i>Rhyzopertha dominica</i>		
35.0	-	-	-	15.7	729.8	0.9832
45.0	11.6	702.8	0.9847	17.1	521.9	0.9808
55.0	11.7	624.3	0.9887	16.8	494.8	0.9854
65.0	11.1	609.4	0.9620	16.7	482.7	0.9890
	<i>Oryzaephilus surinamensis</i>			<i>Tribolium castaneum</i>		
35.0	14.9	393.1	0.9989	-	-	-
45.0	15.3	360.9	0.9983	16.6	547.7	0.9867
55.0	15.5	338.7	0.9985	16.5	458.1	0.9871
65.0	15.6	327.1	0.9994	17.5	371.5	0.9798

the relative humidities considered. *O. surinamensis* is relatively successful at moderate temperatures at all the relative humidities, but it is more successful than the other species at the drier end of the humidity range. By contrast, the population growth of *T. castaneum* is relatively weak under cool and dry conditions. However, as temperature increases at higher relative humidities, population growth rate improve considerably. At the upper range of viable temperatures at humid conditions, *T. castaneum* becomes more successful than even *R. dominica* and is the only species capable of population growth above 38°C .

Relative to the other species, the finite rate of reproduction for *R. dominica* can in part be described by slower immature developmental rates ($1/D$) (Fig. 2) and higher levels of fertility (R_0) (Fig. 3). On the other hand, *S. oryzae* and *O. surinamensis* generally exhibit rapid immature development and short generations rather than high fertility to achieve similar or greater rates of population growth. For example, at 20°C at relative

humidities above 35% r.h., *R. dominica* has a greater net rate of reproduction than *S. oryzae*. However, due mainly to more rapid immature development, *S. oryzae* maintains a greater finite rate of reproduction as temperature increases to 27°C . This strategy is put to even greater use by *O. surinamensis* over practically the entire range of environmental conditions. Its fertility is consistently far less than that of the other species at even the most optimum of conditions. However, low values of R_0 are compensated for by low values of D . In this way, *O. surinamensis* maintains values of similar to or greater than those for the other species. As temperature increases, values of D and R_0 for *T. castaneum* are more affected by levels of relative humidity than they are for the other species. For example, at most temperatures at 45% r.h. values of D for *T. castaneum* are generally similar to those for *R. dominica*. However, at temperatures above 27°C at 65% r.h., only *O. surinamensis* has lower values of D . Values of R_0 at a given temperature also increase dramatically with increased relative

humidity so that above 24°C at 65% r.h. *T. castaneum* is second only to *R. dominica* in levels of fertility. The combination of quicker immature development and higher fertility means that at most temperatures at 65% r.h., *T. castaneum* has similar values for λ to *R. dominica*.

Population growth, wet bulb temperature and implications for pest management

There are potentially important consequences of these results for the use of cooling by aeration as a pest management strategy, especially in an increasingly pesticide-free environment. The insects of most concern must first be *S. oryzae* and second, *R. dominica*. *S. oryzae* has the lowest theoretical thresholds of development and population growth (11.4°C and 14.8°C) (Tables 1 and 2), and at relatively low temperatures such as 18°C, the value of λ is quite significant. Although the degree of relative humidity is not very important (apart from dry conditions, i.e. 35% r.h.), the value of λ does vary from 1.20 [doubling time (t) = 3.8 wks] at 45% r.h. to 1.28 (t = 2.8 wks) at 65% r.h. (Fig. 1). *R. dominica* is not quite so cold tolerant (development threshold = 16.6°C, population growth threshold = 17.5°C). However, at 20°C the value of λ varies from 1.06 (t = 11.9 wks) at 35% r.h. to 1.15 (t = 5 wks) at 65% r.h. Furthermore, it must be remembered that *O. surinamensis*, although it has a higher population growth threshold (19.2°C), is relatively successful at cool dry conditions and has λ values similar to *R. dominica* at just 21°C at humidities as low as 35% r.h.

If increased grain moisture receival limits are to be considered, it is important to be aware of the increasing effect that relative humidity has on the population growth rate of all species as temperatures increase. This is especially the case for *S. oryzae* at cooler conditions. For example, at 22°C values of λ vary from about 0.83 at 35% r.h. [10.1% equilibrium grain moisture content (emc)] to 1.56 at 65% r.h. (13.0% emc). Population growth rates for *T. castaneum* also respond in a similar dramatic manner where at 22°C/35% r.h. population growth is at best negligible but at 22°C/65% r.h., λ = 1.24.

Using limited available data, Desmarchelier (1988) showed that rates of population growth in several stored grain pests, including the four species considered here, are linearly related to wet bulb temperature (T_{wb}) over temperatures ranging from somewhat above the theoretical threshold of population growth to the optimum for population growth. However, with the availability of considerably more information, it has been possible to re-examine this relationship in more detail and to quantify the degree of accuracy achieved by this rule of thumb.

Desmarchelier (1988) used data pooled from a range of temperature and moisture contents to show that a linear relationship exists between λ and T_{wb} for all species at and below the optimum wet bulb temperature for population growth. However, when plots of λ against T_{wb} at each relative humidity are considered, what was a single line has clearly become a family of lines (Table 1). Using these data to calculate the theoretical threshold for population growth (λ = 1) in terms of T_{wb} , the value is found to vary with relative humidity for each species (*S. oryzae* and *T. castaneum*: from 45% to 65% r.h., variation of 2.4 and 2.0 °C. *R. dominica* & *O. surinamensis*: from 35% to 65% r.h., variation of 4.5 and 4.2°C). This is problematic in terms of setting aeration temperatures because it suggests that, though a population at a higher relative humidity may be controlled at a higher T_{wb} , significant rates of population growth occur at the same T_{wb} at lower relative humidities. In the same way, if a lower T_{wb} , equivalent to the population growth threshold at a lower relative humidity were used, unnecessarily high energy inputs

would then be used to control insects at higher relative humidities (Beckett and Evans 1994).

By contrast, the theoretical threshold for population growth over the same range of relative humidities, in terms of dry bulb temperature, varies considerably less (*S. oryzae* and *T. castaneum*: from 45% to 65% r.h., variation of 0.2 and 0.9 °C. *R. dominica* & *O. surinamensis*: from 35% to 65% r.h., variation of 0.4 and 0.4°C) (Table 1). This is due to the fact that the effect of relative humidity on rate of population growth becomes less as temperature decreases towards the minimum theoretical threshold, where it is almost insignificant, as has been demonstrated in the case of *O. surinamensis* (Beckett and Evans 1994).

Also of concern is that, on occasion, different dry bulb temperature/relative humidity combinations can, in some cases, give very different values for λ even though they translate as the same wet bulb temperature. For example, for *S. oryzae*, 25°C/55% r.h. and 30°C/35% r.h. both give approximately 15.5°C T_{wb} , but λ values of 1.84 and 0.86 are recorded at each condition respectively. For *R. dominica*, 30°C/55% r.h. and 36°C/35% r.h. both give 22.8°C T_{wb} , but in this case values of 2.03 and 1.51 are recorded at each condition respectively. Similar examples occur for *O. surinamensis* and *T. castaneum*.

To make accurate predictions of population growth rate for a given species, it would seem more prudent to consider dry bulb temperature and relative humidity rather than wet bulb temperature. For this purpose, contour diagrams of λ values set at intervals of 0.5, incorporating the entire range of the available data for each species, are presented in Figure 4. In this way, if for a particular reason total population control is not considered necessary, aeration conditions can be determined to give the level of control required. In terms of population doubling time (t), where $t = \log_e(2.0)/\log_e(\lambda)$, an insect population halves in one week if $\lambda = 0.5$, is static if $\lambda = 1$, doubles in 1.7 weeks if $\lambda = 1.5$, and doubles in one week if $\lambda = 2$.

Finally, as immature development decreases with increasingly favourable environmental conditions, the likelihood of selection for pesticide resistance increases for all species. However, from the cursory look at the demographic strategies employed by each of the four species, it can be seen that due to its reliance on rapid immature development rather than on high levels of fertility, *O. surinamensis* has a selective advantage for pesticide resistance over the other species. This is especially the case over the moderate temperature range. The increasingly frequent occurrence of resistant strains in Australia over recent years (Allen et al. 1988; Insect resistance to grain protectants in the Victorian central grain handling district 1988; Sproul and Emery 1988; Wallbank 1988) may in part be due to this factor. As temperature increases at high relative humidity, immature development also becomes increasingly rapid for *T. castaneum* relative to other species. So at these conditions, it too is more likely to select for pesticide resistance.

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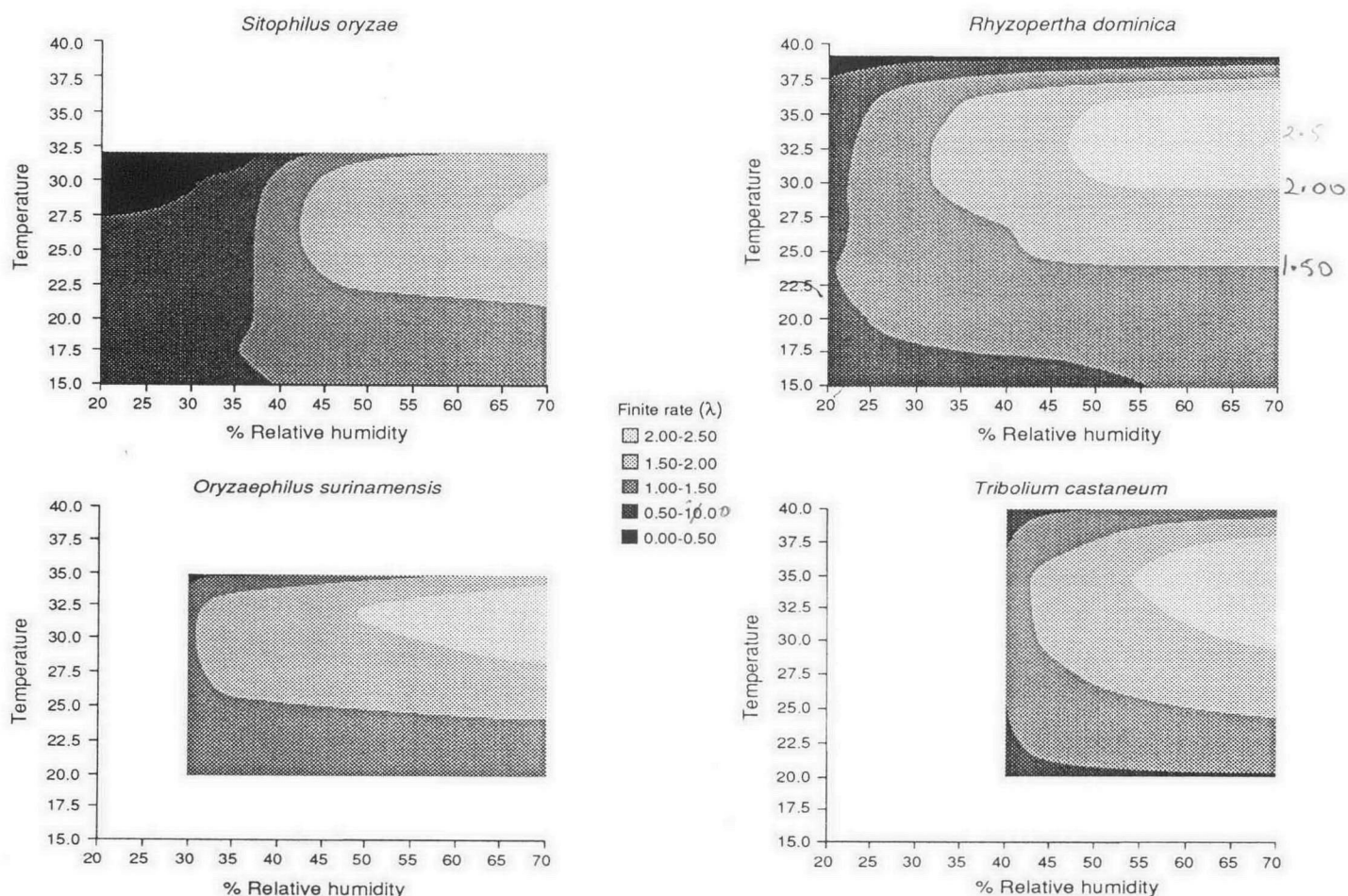


Fig. 4. Contours of weekly finite rate of population increase (λ) for each of four stored grain coleopteran species over a range of temperature ($^{\circ}$ C) and relative humidity (r.h.) combinations. (λ) values below one for *T. castaneum* have been derived from White's (1987) model.

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