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Development of *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) on rice milling components and by-products: Effects of diet and temperature

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ABSTRACT

Development of *Tribolium castaneum* (Herbst), the red flour beetle, was assessed on different rice components and their various by-products (i.e., diets) commonly found in rice mills, in two separate experiments. In the first experiment, eggs did not develop through to the adult stage on rough rice hulls, paddy rice dust, and milled rice dust, while eggs developed to the adult stage to some extent on rice flour, milled whole kernels, brown rice, milled broken kernels, and bran. For the diets where development occurred, the lowest percentage was on brown rice, and adults that emerged on brown rice had smaller elytra compared to adults emerging on the other diets. In the second experiment, 1–2-day old neonates were exposed on the diets listed above and held at 22, 27, 32, and 37 °C. At all temperatures, development to the pupal and adult stages was slowest on rice flour. At 22 °C, development to those stages took about twice as long compared to development at 27 °C. As temperature increased developmental times were reduced. Even though neonates developed slowest on rice flour adult emergence rates were not affected. Predictive models were used to estimate potential population development on the diets. At 22 and 27 °C, adult size as measured by elytra length was greatest when they developed on bran, while body weight was generally lowest for adults that developed on brown rice. Results show that *T. castaneum* can utilize rice components and by-products produced during the rice milling process, although not all components or by-products were optimal for development, and emphasis should be placed on cleaning and sanitation to remove food sources to limit infestations. Mill managers can use these results to show the importance of sanitation, and potentially improve overall pest management programs inside the mill.

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1. Introduction

Rice is an important crop world-wide, and in the Unites States it is primarily grown in the south-central states of Arkansas, Louisiana, east Texas, southeastern Missouri, along the eastern side of the Mississippi river, and in the north San Joaquin valley in California. Depending on the specific location, planting date, and environmental conditions, rice can be harvested from late-July and early August to late September and early August (Arthur et al., 2011; Yang et al., 2017). After harvest, rice is stored as rough or paddy rice, and then sent to mills where it is broken down through a multi-step process. In brief, the husk or hull is removed to produce brown rice, which is further milled by removing the bran and germ layers to produce milled rice. Additional processing is done to produce polished white rice from milled rice, or to grind milled rice to produce rice flour. In addition to the different types of rice, there is a range of by-products also produced during milling (Table 1) which could potentially be exploited by stored product insect pests.

One of the most important stored product insects infesting wheat mills and rice mills is the red flour beetle, *Tribolium castaneum* (Herbst) (Campbell et al., 2010a,b; Hawking et al., 2013; Buckman et al., 2013; Campbell et al., 2015; Toko, 2015, Arthur et al.,

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Table 1
A description of rice components and by-products (diets) obtained from a local rice mill in Northeast Arkansas.

	Diet	Brief Description
Rice Components	Rough Rice	Rice in its natural form still covered by the hull or husk
	Brown Rice	Rice with hull removed but bran layer intact
	Milled Whole Kernels	Brown rice that the germ and bran layers polished off
	Rice Flour[a]	Finely milled white rice
Rice By-Products	Rough Rice Hulls	Outer shell covering the kernel, removed during the milling process
	Rough Rice Dust	Dust that collects in machinery as rice is milled from rough rice to brown rice
	Rice Bran	Produced when rough rice is milled down to white rice
	Milled Broken Kernels	Same as Milled Whole Kernels, but kernels are broken
	Milled Rice Dust	Dust that collects in machinery during the polishing process

[a] Experiment 1, rice flour purchased from Arrowhead Mills, CO; Experiment 2, rice flour obtained from a commercial rice mill.

2015). This insect was first noted by Good (1936) as the most important pest of wheat mills in Kansas. It is commonly associated as a pest of wheat flour, but it can feed on a variety of processed grain products, including some whole grains such as brown rice (Kavallieratos et al., 2015).

Many studies in recent years have addressed population dynamics of various stored product insects on wheat, including the development of an expert system to manage bulk stored wheat (Flinn et al., 2007). However, comparatively less emphasis has been given to predicting insect population growth in stored rough rice. Yang et al. (2017) developed a web-based system to help manage stored product insects, primarily *Rhyzopertha dominica* (Fab.), the lesser grain borer, and *Sitophilus oryzae* (L.), the rice weevil, in stored rough rice. This system was used to predict population growth in unaerated and aerated rough rice stored in the south central United States (Arthur et al., 2011). Population dynamics and development rates are likely to be very different in structures where grains are milled compared to storage of raw grains. In mills beetle diet is more varied, temperature and other environmental conditions are more variable, and food resources are patchier (Campbell et al., 2015) compared to bulk stored grain. There have been studies documenting population dynamics and population increases in wheat and rice mills following fumigations with methyl bromide or sulfuryl fluoride (Campbell et al., 2010a,b; Buckman et al., 2013; Campbell et al., 2015). It appears that *T. castaneum* population dynamics in rice mills is strongly influenced by seasonal temperature changes, and populations increased at a slower rate in rice mills compared to wheat mills (Buckman et al., 2013), perhaps due to greater seasonal variation in temperature but also perhaps related to the diet. There has been little published research to date on how the environment within a rice mill impacts *T. castaneum* development, specifically how temperature and rice components and by-products impact development.

The time required for egg to adult development for *T. castaneum* depends on a variety of factors, including temperature, moisture, and diet. Hagstrum and Milliken (1988) estimated development time ranging from 22 to 42 days, with temperature being the most important factor affecting development rate. Baldwin and Fasulo (2003) stated that based on temperature and relative humidity (r.h.) the developmental range was 40–90 days. Temperatures under which *T. castaneum* can develop range from about 22 to 35 °C (Howe, 1965; Fields, 1992). A study by White (1987) stated optimal conditions for development of *T. castaneum* on whole wheat grains were 35 °C and 60% r.h. There is little development below 15 °C or above 40 °C (Fields, 1992).

In addition to the effects of temperature and diet on development time and probability of reaching the adult stage, developmental conditions can also impact adult fitness traits of individuals that develop successfully. In insects, poor nutrition during development typically leads to adults with decreased size, less progeny production, and shorter lifespan (e.g., Scriber and Slansky, 1981; Awmack and Leather, 2002; Colasurdo et al., 2009; Dimitriew and Rowe, 2011). Temperature during development can impact adult size and other fitness traits as well and interact with the effects of diet. Lower temperatures often result in slower development times but larger adults (Atkinson, 1994; Atkinson and Sibly, 1997), but there can be intermediate optimal temperatures where adult size is maximized (David et al., 1994; Karan et al., 1998). However, the effects of temperature and diet can have complex interactions across developmental stages. For example, warmer temperatures and yeast-rich diet during development improved *T. castaneum* reproduction (Scharf et al., 2015). Adult size, typically measured by elytra length and body weight, has been correlated with fecundity for many insect species and while not capturing the full fitness consequences is still considered a good indicator of fitness (Knapp and Knappova, 2013).

Studies evaluating development of stored product insects on rice with different levels of milling are limited. McGaughey (1970) conducted studies with stored product insects, including *Tribolium confusum* Jacquelin duVal, the confused flour beetle, and showed decreased progeny production as the percentage of bran removed from different rice varieties increased and McGaughey (1974) found this also reduced progeny production. Kavallieratos et al. (2015) demonstrated that *T. castaneum* could develop on brown rice. However, there have not been any studies to evaluate development on rice with different levels of milling and on the by-products that are produced. These by-products, such as hulls and removed bran are potentially important resources in maintaining resident pest populations in mill buildings and equipment since *T. castaneum* tends to exploit small patchy food accumulations (Campbell and Runnion, 2003). The objectives of this study were to determine: 1) *T. castaneum* development on different rice components and by-products (hereafter termed diets) produced during the milling process, 2) Impact of temperature on development on different diets, 3) If adult fitness, as measured by body size, is affected by diet and developmental temperature, and 4) Estimated potential population growth on different diets at different temperatures. Related experiments are described and discussed in this publication.

2. Materials and methods

2.1. Experiment 1

This study was conducted at Arkansas State University, Jonesboro, AR, USA. Rough rice or paddy rice and brown rice were obtained from a local mill, while rice flour was purchased from a commercial source (Arrowhead Mills, Boulder, CO, USA). These are considered as “components” because rough rice was the beginning product in the milling process, and brown rice and rice flour were distinct end products. Rough rice hulls, rough rice dust, milled broken kernels, and milled whole kernels were considered as “by-products” because they were produced during the milling process.

All by-products were obtained from the same rice mill that provided the rough rice and the brown rice.

The individual experimental unit was an 18.5 ml vial (Bioquip Products, Inc., Rancho, Dominguez, CA, USA) that contained ~ 1 g of one of the rice diets. The *T. castaneum* used for the study was a laboratory colony that originated from the USDA-ARS Center for Grain and Animal Health Research, (CGAHR). Manhattan KS, where it had been maintained for more than 30 years. *T. castaneum* was reared on a diet of 95% whole-wheat flour and 5% Brewer's yeast at 25 °C and 65% r.h, before exposure in the experiments.

Replications of each of the nine diets were performed, in blocks consisting of trays with six replicate vials of each of the diets, with one tray (block) prepared daily for eight days (58 replicate vials total). For this experiment, the initial exposure stage was eggs, which were obtained by first placing about 20-mixed sex one-to-two-week adults in a 0.24 L glass jar containing about 300 mg of white flour which had been sifted through a #50 sieve (openings of 0.30 mm). These adults could oviposit in the flour for a minimum of 48 h, then adults were sifted off the flour using a # 12 sieve (openings 1.7 mm). Aliquots of 100–200 mg of flour were examined to remove eggs. Those aliquots were placed into a glass Petri dish, and the dish placed under a stereo microscope. The eggs were visible and could be removed using a single-hair brush. After one of the trays were prepared, a single egg was placed in each of the vials and transferred to rearing room at Arkansas State University and held at 25 °C and 65% r.h.

After 8 weeks, the trays were removed from the rearing room and frozen at −20 °C. After about 3 weeks, the contents of each vial were emptied into a dish, and if an individual was not detected (egg did not develop), or if the egg had progressed to the larva, pupa, or adult stage, it was recorded. For each adult, the right elytron was measured to a precision of 0.01 mm using a dissecting microscope [Zarbeco, LLC Creative Imaging Solutions (ZC105A USB 2.0 1.3 Megapixel Camera and Video Toolbox Pro 2.06.3(6A) Randolph, NJ, USA)] by measuring from the apex to the base of the right elytron. The dry body weight of all adults was obtained by placing them in a Fisher Scientific heating and drying oven, for 8 h at 100 °C. Weights of the dried beetles were measured using a Shimadzu AUW220D scale (Nakagyo-ku, Kyoto, Japan) to a precision of 10^{-2}mg.

To determine if a diet was suitable for development, the percentage of eggs that progressed to any life stage (larva, pupa or adult) was compared among the nine diets using a Chi-Square test (SAS Institute version 9.2, Cary, NC, USA). Since only five diets had eggs that developed, a second Chi-square test was conducted among those five diets to see if there were differences in percentage development for each of the life stages. The Mixed Procedure of SAS was used to determine differences in mean elytral lengths and dry weight of adults, and means were separated using a Tukey test to determine significance at $P < 0.05$.

2.2. Experiment 2

Time Block 1. This study was conducted at the ARS facility in Manhattan, KS, and was based on the results obtained in Experiment 1. About 2–3 kg each of brown rice, rice bran, whole kernels of milled rice, and broken kernels of milled rice, were obtained from the same commercial rice mill as specified in Experiment 1 (Table 1). Rice flour was obtained from a second commercial mill in Arkansas. Three incubators (Percival Scientific, Perry, IA, USA) were set to 22, 27, and 32 °C, to simulate temperatures that could be present during normal operations of a rice mill. The r.h. was set at 60% for all temperatures. The individual experimental unit was an 18.5 ml vial that contained 1 g of one of the five diets listed above. There were 25 replicate vials for each diet-temperature combination, which were held in groups of 25 in a vial rack for each diet.

The *T. castaneum* used in the study were from the same original source as in Experiment 1 and reared under the same conditions. In contrast to Experiment 1, neonate larvae (1-2- day-old larvae) were used as the initial stage rather than eggs, which should remove the potential effects of temperature on egg hatch. To obtain neonates for the study, about 50 1-2-week-old mixed sex adults were obtained from the colony and placed in a 0.95 L jar containing about 300 g of flour sifted through a #60 sieve (openings of 0.25 mm). The flour was sifted to this size for ease of neonate collection after egg hatch. The adults were held on the flour for about 48 h at 27 °C and 60% r.h. inside the incubator, then removed from the jar as described above. After 24 h, allotments of about 200–300 mg of flour were removed from the jar and placed in a Petri dish to collect the neonates. One neonate was placed into each vial using a camels-hair brush with a single hair. Once all neonates were placed into vials, the vials were divided into lots of 75 each so they could be held in each of the four incubators.

After two weeks, each vial was checked daily. Once a larva had pupated, that date was recorded, and the vials were retained to record the date of adult emergence. After the adult stage was reached the date was recorded and the vials were frozen at −18 °C. If an adult was present, the vial and its contents were stored in a freezer until the vials could be shipped to Arkansas State University, Jonesboro, AR, where further measurements of the adult elytra were done as described for Experiment 1.

Time Block 2. This block consisted of 25 additional replicates of the same rice diets and temperatures as in Time Block 1, but an additional temperature of 37 °C, 65% r.h., was added with 50 replications in a separate incubator set at 37 °C. Eggs were collected, the diets were divided into vials, and neonates were collected as described for Block 1. Development was assessed as described for Block 1.

2.3. Statistical analysis

For data analysis, both time blocks in Experiment 2 were pooled together. PROC Mixed in the Statistical Analysis System was used to determine significance of main effects temperature and diet with respect to time to pupation or adult emergence. A one-way analysis was used to determine significance between diet and emergence dates, and LSMeans with Tukey adjustment was used to separate means. Another two-way test in PROC Mixed was performed to determine if there were differences in the mean elytral lengths among temperatures and diets. A Chi-Square test was done to determine significance of percentage adult emergence among temperatures and diets.

2.4. Population predictions

The longer-term impacts of temperature and diet on population growth or population size over a year (365 d) was estimated for all five diets at each temperature from the second experiment (both Blocks). Data for adult emergence over time at each of the temperatures and diets were used to model population growth of *T. castaneum*. Since no survivorship data was calculated we used a cumulative summation for these populations with no death rate; however, adult emergence data also considers the percentage of adults that emerge from the total tested, so this is also an influential factor in calculating population growth for these diets and temperatures. To model population growth over a year, we used the original data for adult emergence over time as our first generation of females. Each generation was confined to reproduce dependent on the original emergence timing for the first generation of females. For example, if females emerged from days 52–99, the next generation would emerge from days 104–151. A given female that emerged in the original, first generation produced one female to the next generation. That female then produced another female for the next generation and so on, until 365 days, or 1 year, was reached. A generalized linear mixed model using GLIMMIX Procedure in SAS was used to assess if the diets and generations lead to differences in the cumulative sum of the population, using diets and generation as main effects, plus the diet and generation interaction effect.

3. Results

3.1. Experiment 1

There were significant differences in percentage development among the nine diets: ($\chi^2 = 202.3$, $P < 0.01$, Table 2). Eggs did not develop on rough rice, or on the diets rice hulls, rough rice dust or milled rice dust. Eggs hatched on brown rice, and the diets bran, milled broken kernels, milled whole kernels, and rice flour, and *T. castaneum* developed to either the larval, pupal or adult stage. Among those five diets there were significant differences in the number of eggs that hatched ($\chi^2 = 12.0$, $P = 0.02$); bran had the highest percentage of egg hatch (81%) and brown rice had the lowest percentage of egg hatch (34%).

For the diets in which *T. castaneum* eggs developed there were significant differences in percentages of larvae ($\chi^2 = 91.4$, $P < 0.01$), pupae ($\chi^2 = 22.2$, $P < 0.02$) and adults ($\chi^2 = 166.9$, $P < 0.01$, ChiSq tests done on raw data). Brown rice had the highest proportion of larvae (13%), whereas bran, milled whole kernels, milled broken kernels and rice flour had lower proportions of larvae. Milled whole kernels had the highest proportion of eggs that reached the adult stage (71%), whereas the lowest adult emergence was on brown rice (Table 2). For the five diets that had development, pupae and larvae were present in all of them except for milled whole kernels, where larvae were present, but no pupae were observed (Table 2).

There were no significant differences in elytral lengths among the adult beetles reared on the five diets that supported egg to adult development ($F = 2.15$, df = 4, 119, $P = 0.07$). The elytral lengths ranged from 2.03 ± 0.08 mm when reared on brown rice to 2.25 ± 0.05 mm when reared on rice flour (Table 3). However, there was a significant difference in the mean body weights of beetles developing on the diets ($F = 3.33$, df = 4, 1119, $P = 0.013$) (Table 3). *T. castaneum* reared on brown rice had lower body weights than beetles reared on the other four diets (Table 3). However, only seven beetles reared on brown rice were measured, so the lower weight might be an artifact due to small sample size.

An analysis was done to correlate body weight with elytral lengths for each rice diet that supported development. The two variables were not correlated for brown rice or rice flour ($P = 0.49$, $r = 0.32$, $P = 0.73$, $r = -0.06$), respectively. There was a significant positive correlation between the body weight and elytral length for adults reared on bran, milled broken kernels, and milled whole kernels ($P < 0.01$, $r = 0.52$; $P = 0.027$, $r = 0.41$; $P = 0.035$, $r = 0.36$, respectively).

Table 2
The percentages of *T. castaneum* eggs that had developed to larvae, pupae, and adults after eight weeks on nine rice components and by-products (N = 48 for each diet).

Diet	Larvae	Pupae	Adults
Components			
Rough Rice	0	0	0
Brown Rice	13	6	15
Milled Whole Kernels	4	0	71
Rice Flour	4	13	63
Rice By-Products			
Rough Rice Hulls	0	0	0
Rough Rice Dust	0	0	0
Bran	6	6	67
Milled Broken Kernels	4	2	58
Milled Rice Dust	0	0	0

Table 3
Body weight (mean ± S.E.) and elytral lengths (mean ± SE) of adult *T. castaneum* on five rice diets. Means between diets within columns followed by lower case letters are different ($P < 0.05$, LS Means under Proc Mixed in SAS).

Diet	N	Body Weight (mg)	Elytron Length (mm)
Brown Rice	7	0.43 ± 0.04b	2.03 ± 0.08a
Bran	32	0.61 ± 0.02a	2.21 ± 0.03a
Milled Whole Kernels	34	0.60 ± 0.02a	2.17 ± 0.04a
Milled Broken Kernels	28	0.61 ± 0.03a	2.21 ± 0.03a
Rice Flour	30	0.59 ± 0.02a	2.25 ± 0.05a

3.2. Experiment 2

The main effects temperature and diet, and the interaction between them, were significant for days to pupation at $P < 0.01$ ($F = 2257.3$, df = 3, 725; $F = 60.3$, df = 7, 725; $F = 6.1$, df = 12, 725, respectively). At each temperature, time to pupation was longest for neonates exposed on rice flour (Table 4). At 22 °C, the time difference was about two weeks greater for exposures on rice flour compared to the other diets. As temperature increased, the time gap for development on rice flour compared to brown rice and the diets narrowed, but was still significantly different even at 27 °C. At 22 °C, the time range for pupation on all diets ranged from 61.9 to 80.6 days, but at 27 °C the time range was reduced by more than 50% (range was 22.5–36.1 days). There was no difference in developmental time to the pupal stage between 32 and 37 °C on any diet.

The main effects of temperature and diet, and the interaction, were also significant for days to adult emergence at $P < 0.01$ ($F = 2270.2$, df = 3, 725; $F = 52.4$, df = 7, 725; F = 2.6, df = 12, 725, respectively). Developmental patterns followed those observed for pupae, with time to adult emergence greatest for neonates exposed on the rice flour, at all temperatures (Table 5). In some instances, the fastest developmental times were recorded for neonates exposed on bran. With respect to temperature, there was again about a 50% decrease in time to adult emergence on all diets as temperature increased from 22 to 27 °C, some indications of decreased developmental times for the next temperature increase from 27 to 32 °C, and no difference in developmental time to adult emergence for neonates exposed on any diet at 32 versus 37 °C.

A Chi-Square analysis was done on the data for percentage adult emergence using PROC Frequency in SAS. There were no significant differences in percentage emergence with respect to temperature ($P \geq 0.05$); Chi-Square values ranged from 0.10 to 0.42, and the lack of significance is clear from the data presented in Table 6. When diets were analyzed by temperature, only rice flour was significant ($P < 0.01$), mainly because of the low value at 22 °C. Even though

Table 4
Days to pupation (mean ± SE) of *T. castaneum* neonates exposed on five rice diets at four temperatures. Means for pupation days at a temperature followed by lower case letters within columns are different. Means for differences between diets at a temperature followed by different capital letters between rows are different ($P < 0.05$, LS Means under Proc Mixed in SAS).

Diet	22 °C	27 °C	32 °C	37 °C
Brown Rice	65.1 ± 2.5bA	29.2 ± 0.7bB	17.8 ± 0.3bC	16.9 ± 0.3bcC
Bran	62.9 ± 1.8bA	22.5 ± 0.6cB	16.6 ± 0.2bcC	15.5 ± 0.3cC
Milled Whole Kernels	64.9 ± 1.8bA	28.7 ± 0.5bB	18.9 ± 0.3bC	21.9 ± 0.4aC
Milled Broken Kernels	61.9 ± 1.7bA	27.2 ± 0.7bcB	13.3 ± 0.3cD	17.4 ± 0.4bC
Rice Flour	80.6 ± 2.1aA	36.1 ± 0.6aB	24.0 ± 0.6aC	22.0 ± 0.6aC

Table 5
Days to adult emergence (mean ± SE) of *T. castaneum* neonates exposed on five rice diets at four temperatures. Means for pupation days for diets at a temperature followed by lower case letters within columns are different, means for differences between diets at a temperature that are followed by different capital letters between rows are different ($P < 0.05$, LS Means under Proc Mixed in SAS).

Diet	22 °C	27 °C	32 °C	37 °C
Brown Rice	78.7 ± 2.6bA	36.0 ± 0.8bB	21.6 ± 0.3bcC	21.0 ± 0.3bcC
Bran	75.4 ± 2.1bA	31.3 ± 0.3cB	20.3 ± 0.4cC	19.2 ± 0.3cC
Milled Whole Kernels	79.8 ± 1.7bA	36.4 ± 0.6bB	23.2 ± 0.4bC	25.9 ± 0.5aC
Milled Broken Kernels	75.3 ± 1.7bA	34.1 ± 0.6bcB	21.5 ± 0.4bcD	21.4 ± 0.4bcC
Rice Flour	90.7 ± 3.3aA	43.8 ± 0.6aB	29.1 ± 0.7aC	26.5 ± 0.6aC

Table 6
Percentage of adult emergence on five diets at four temperatures.

Diet	22 °C	27 °C	32 °C	37 °C
Brown Rice	74	84	76	84
Bran	66	88	82	70
Milled Whole Kernels	76	84	90	74
Milled Broken Kernels	76	76	80	84
Rice Flour	68	92	70	86

time to adult emergence varied significantly for temperature and diet, the percentage of adults that emerged was similar across temperature and diets, regardless of the time it took for the neonate to emerge as an adult.

Elytra length was significantly related to developmental temperature ($F = 3.4$, df = 3,734, $P = 0.01$), but not to diet, and the interaction was significant ($P < 0.05$). However, when data were analyzed with respect to temperature, there were no significant differences for any of the diets ($P \geq 0.05$, Table 7). At 22 and 27 °C, elytral lengths were greatest in adults emerging from bran, while at 32 °C adults emerging on broken milled white rice kernels had the greatest elytral lengths. Results for body weights of emerged adults was significant at $P < 0.001$ for temperature, diet, and the interaction ($F = 11.1$, df = 3, 687; $F = 7.1$, df = 4, 687; $F = 20.5$, df = 12, 687, respectively). There was not a consistent pattern of body weight increasing with temperature or for an intermediate temperature to produce heaviest body weight. The order of greatest body weights was generally different at each temperature, but at 22, 27, and 32 °C weights were lowest for adults emerging from brown rice (Table 8).

A correlation analysis was done on elytral lengths and body weight by combining all data for temperature and examining each diet separately. Elytral lengths and body weight were not correlated for adults emerging on brown rice ($P = 0.16$, $r = 0.12$). There were positive correlations between elytral lengths and body weights for bran, milled whole kernels, milled broken kernels, and rice flour ($P < 0.001$, $r = 0.30$; $P < 0.001$, $r = 0.22$; $P < 0.001$, $r = 0.36$, and $P < 0.001$, $r = 0.35$, respectively).

3.3. Population predictions

Projecting adult female populations for a year provides a comparison of how populations on the different diets at different temperatures will change in size over time. At all temperatures, the interaction effect of diet and temperature was significant (22 °C: $F = 6.9$, df = 17, 495, $P < 0.0001$; 27 °C: $F = 35.8$, df = 40,577, $P < 0.0001$; 32 °C: $F = 109.4$, df = 70,721, $P < 0.0001$; 37 °C: $F = 34.4$, df = 70, 714, $P < 0.0001$). After the first generation (original data) all other generations had significant differences among diets (Fig. 1; $P < 0.0001$). In addition, all diets had significant increases in population sizes ($P < 0.0001$). At 22 and 37 °C, broken kernels had the highest population growth over a year and rice flour had the lowest growth over a year (Fig. 1). At 27 and 32 °C, bran had the lowest population growth while brown rice had the highest growth at 27 °C and whole kernels had the highest at 32 °C. Beetles also performed well on whole kernels at 27 °C, with the second highest population growth over a year. Interestingly, beetles on bran had moderately good growth rates at 22 and 37 °C relative to other diets.

4. Discussion

Tribolium castaneum is a generalist feeder on a variety of grain products in addition to wheat flour; in addition, it can feed on flours of other commodities and also on processed food products. This study is the first published study that examines development of *T. castaneum* on components of rice and their by-products (diets) produced during the rice milling process. McGaughey (1970) conducted studies with stored product insects, including the congeneric *T. confusum*, and showed decreased progeny production when the percentage of bran removed from different rice varieties increased from 74 to 100%, indicating that the degree of milling affected insect development on the grain that remained. In a related study (McGaughey, 1974), the degree of milling also affected progeny production. In our study, we found that there were rice components and by-products that *T. castaneum* did not develop on (rough rice, rough rice hulls, rough rice dust, milled rice dust), but on the components where development did occur there was not a significant impact of milling on *T. castaneum* development, with the possible exception of rice flour.

Previous studies with insecticide research showed that *T. castaneum* would develop on brown rice (Kavallieratos et al., 2015). All diets tested in Experiment 2 of this study supported development to some extent, regardless of temperature. A review by Gul et al. (2015) noted that rice bran was a source of nutrients, proteins, dietary fiber, antioxidants, oils, and sterols, among other compounds, and is commonly used as a component in animal feeds.

Table 7
Mean elytral lengths (mean ± SE) of adults emerging from neonates exposed at four temperatures on five diets. Means within colums followed by different lower case letters are different ($P < 0.05$, LS Means under Proc Mixed in SAS).

Diet	22 °C	27 °C	32 °C	37 °C
Brown Rice	2.27 ± 0.02b	2.27 ± 0.02b	2.37 ± 0.03b	2.24 ± 0.02b
Bran	2.39 ± 0.04a	2.45 ± 0.02a	2.45 ± 0.02b	2.35 ± 0.02b
Milled Whole Kernels	2.20 ± 0.02b	2.27 ± 0.03b	2.31 ± 0.02b	2.26 ± 0.02ab
Milled Broken Kernels	2.30 ± 0.03b	2.29 ± 0.03b	3.12 ± 0.08a	2.29 ± 0.02b
Rice Flour	2.21 ± 0.03b	2.37 ± 0.02b	3.23 ± 0.87a	2.25 ± 0.02b

Table 8
Body weights (mean ± SE) of adults emerging from neonates exposed at four temperatures on five diets. Means for diets at a temperature followed by lower case letters within columns are different, means for differences between temperature for a diet followed by different capital letters between rows are different (P < 0.05, LS Means under Proc Mixed in SAS).

Diet	22 °C	27 °C	32 °C	37 °C
Brown Rice	0.42 ± 0.03bB	0.54 ± 0.02bB	0.59 ± 0.05bB	1.09 ± 0.01aA
Bran	0.63 ± 0.03abA	0.68 ± 0.07aA	0.71 ± 0.03aA	0.78 ± 0.03bA
Milled Whole Kernels	0.63 ± 0.06abA	0.52 ± 0.02bA	0.59 ± 0.04bA	0.59 ± 0.06cA
Milled Broken Kernels	0.59 ± 0.02abB	0.32 ± 0.03cD	0.84 ± 0.03aA	0.47 ± 0.03cC
Rice Flour	0.78 ± 0.04abA	0.68 ± 0.02aB	0.77 ± 0.02aA	0.34 ± 0.03cC

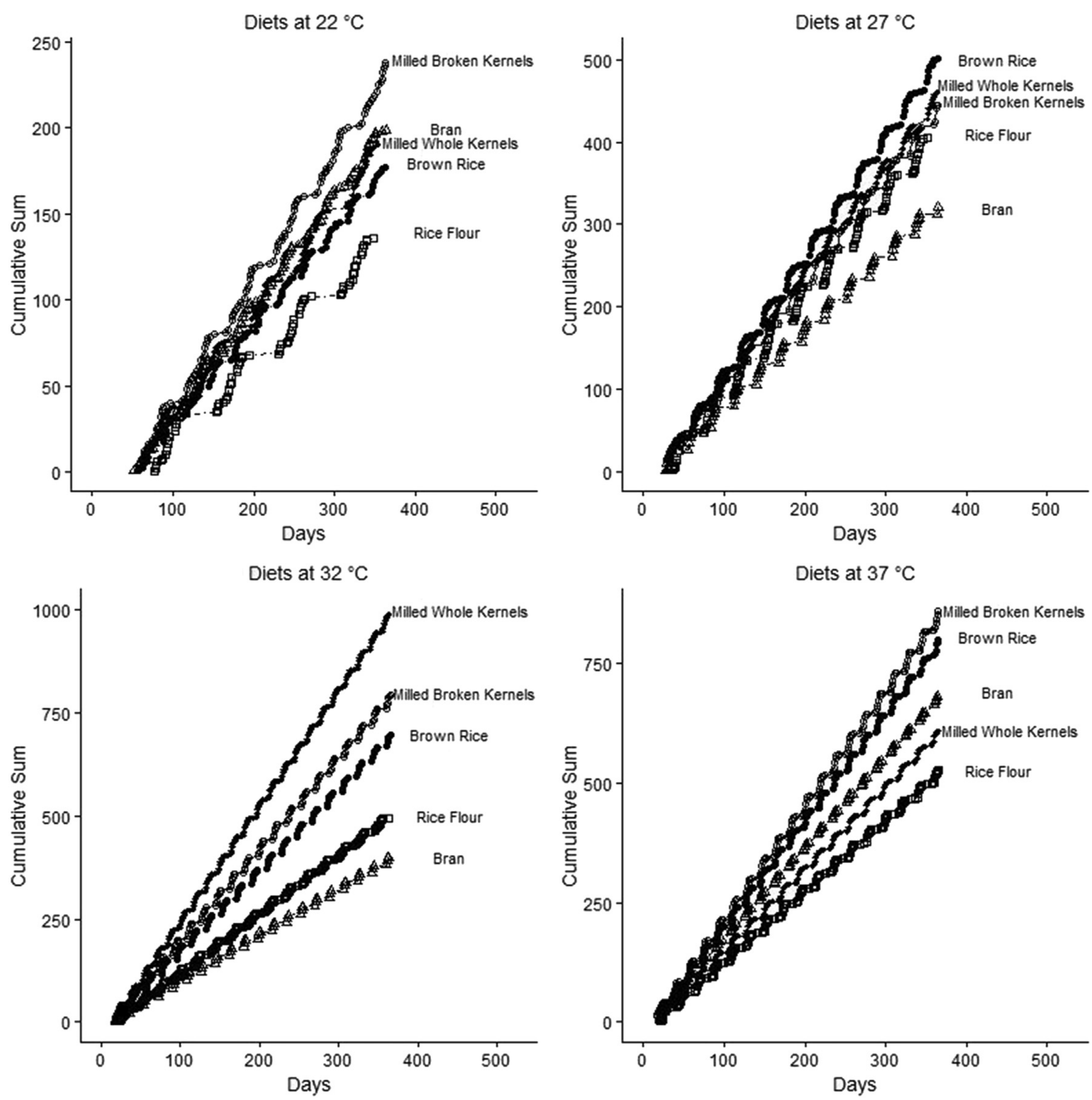

Fig. 1. Population projections on adult emergence over time. Graphs represent population projections for one year, or 365 days (x-axis), when considering the emergence data of adults at each temperature. The y-axis is the cumulative sum of the population over time.

Thus, it is not surprising that *T. castaneum* could develop on rice bran. Also, in our studies *T. castaneum* generally developed faster on bran compared to other diets, had longer elytra, and occasionally greater body weights, which could be an indicator of quality of bran as a diet.

Rice flour can be used as a substitute for wheat flour to produce breads and pastas for individuals with Celiac disease who cannot digest wheat gluten (Pérez-Quirce et al., 2017). Producing dough with acceptable quality is difficult, and in addition, protein supplements are often added to the rice flour to improve taste, nutrition, and cooking properties (Phongthai et al., 2017). In our study, developmental times were longer on rice flour than on milled rice which was surprising because the parent colony was reared on brown rice, but the original source was a colony that had been reared for more than 30 years on wheat flour. Perhaps small amounts of bran are removed when milled rice is ground further to produce flour. However, even though development was prolonged, neonates exposed on rice flour still emerged as adults at the same approximate percentages as adult emergence on the other diets, indicating that *T. castaneum* can adapt to sub-optimal diets. Milled whole and milled broken kernels were suitable for development. The texture of the rice flour may have also been a factor affecting development rate. All diets listed above, except perhaps milled broken kernels, could be packaged and sold separately, which suggests they all are vulnerable to infestation by *T. castaneum* at the retail level. These diets are also likely to accumulate in equipment and structures within rice mills and be resources to support *T. castaneum* infestations.

Although *T. castaneum* was able to complete development on many rice fractions, a slower development time can have negative fitness effects that are not detectable under laboratory conditions. Risk of mortality can increase the longer the development period as an immature. Delaying time to mating for adults can also reduce progeny production (Gerken and Campbell, 2018). Other studies have shown that different types of sub-optimal diets (Liu et al., 2004; Athanassiou et al., 2017) can have significant impacts on the net reproductive rates of stored product pest species over a longer time period. Although *T. castaneum* is able to develop on sub-optimal diets, the increased time to pupation and adult emergence ultimately affects projected population growth which can impact their potential impacts as a pest in a food facility. This longer developmental time may also increase efficiency of pest management techniques by allowing treatments to be more effective or chemicals such as insect growth regulators to affect younger developmental stages over a longer time.

The temperature effects noted in this study were a bit surprising, especially the prolonged development of *T. castaneum* at 22 °C. This temperature was well within the zone of favorable temperatures for development of this species (Park and Frank, 1948; Howe, 1956), although it is an established fact that developmental time for *T. castaneum*, and most stored product insects, decreases with increases in temperature (Park and Frank, 1948; Howe, 1956) up to about 35 °C, after which further increases in temperature negatively affect development. Although in our study the increased developmental times did not result in decreased adult emergence, results suggest that even slightly cool temperatures during storage could potentially be used as a management strategy for protection of finished milled rice products, such as brown rice, bran, or rice flour. Levels of mortality during development due to predation, disease, or mechanical damage under conditions found in mills is unknown. Research has previously established the feasibility of cold temperatures as a disinfestation strategy, which would be useful for organic pest management (Flinn et al., 2015). Although the lower limit of development for most stored product insects is around 15 °C (Howe, 1965; Fields, 1992), it may be possible to limit development on extraneous rice by-products using slightly higher temperatures than the lower developmental threshold, where insects may be present and accumulate in areas where finished products are stored before shipment at warmer temperatures.

The temperature effects also had an impact on the population projections of the five diets examined. Temperature has been shown to play a large role in the development of insects (Angilletta, 2009). Insect population growth curves are typically substantial increases in population numbers over time due to their quick development time and large numbers of offspring. Age- or stage-based modeling often considers both fecundity and survivorship (Leslie, 1945). Our population growth calculations using only adult emergence find that given enough time for full adult emergence, populations on any rice diet and at any temperature show population increases, but some diets were more preferable in terms of population growth rates. At different temperatures, insects performed differently on the rice diets in relation to one another; for example, at 27 and 32 °C, bran has the lowest growth rate, but rice flour has the lowest growth slope at 37 °C. Further, broken kernels have the highest growth slope at 22 and 37 °C but whole kernels have the highest growth slope at 32 °C. Since we assigned each female to increase the population by only one female in the next generation with no death rate, these growth projections based on the emergence rates and percentages highlight the importance of considering both food source and environmental variables when evaluating life history characteristics in insect populations. Temperature has a large impact on the variability of which rice by-product provided the best nutritional value for a quick emergence time, which ultimately lead to faster growth over a single year period.

Previous research with wheat milling and rice milling facilities has shown that infestations of *T. castaneum* can be present in the milling environment (Campbell et al., 2015). However, it seems that populations of *T. castaneum* in wheat mills tend to be more self-contained within the mill and to increase throughout the year (Campbell et al., 2010a,b; 2015), whereas in rice mills there appears to be more immigration and emigration into the facility and populations increase and decrease with season (Buckman et al., 2013). In the Buckman et al. (2013) study, temperatures and trap catch of *T. castaneum* inside the mill closely matched those outside the mill, and this pattern was not apparent in wheat mills. Rice mills tend to have fairly wide ranges of seasonal temperature conditions, which results presented here indicate will have large impacts on the ability of red flour beetle to develop on rice diets. The combination of presence of milled rice diets that do not favor development and low temperatures during certain portions of the year may contribute to lower population growth rates in rice mills relative to wheat mills.

The phase-out of the fumigant methyl bromide has led to increased interest in the use of aerosol insecticides and residual surface treatments for control of stored product insects inside rice mills (Arthur, 2012; Buckman et al., 2013; Campbell et al., 2015), which places more emphasis on targeted treatments rather than whole-plant treatments. Data on *T. castaneum* development on rice diets, along with effects of temperature, would seem to be important inputs when designing integrated pest management programs for rice milling facilities, as the species composition and diversity varies within different areas of milling facilities (Campbell et al., 2015). Emphasis should also be placed on sanitation and cleaning, as accumulated rice milling debris can support pest population development in the building structure and can also reduce insecticidal efficacy of aerosols and contact insecticides (Arthur et al., 2014, 2017). Information from our study can also be used to prioritize sanitation efforts to emphasize areas where the potential diets most favored by *T. castaneum* as likely to accumulate.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jspr.2018.11.001.

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