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The effects of population densities and feed diets on some *Tribolium castaneum* Herbst life parameters

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Abstract

The effects of population densities (10, 25, 50 and 100 adults/50g) and three feed diets on several life parameters (first emergence, development rate, number of progeny and body weight) of *T. castaneum* progeny were assessed. In each type of diet and population density unsexed adults were allowed to feed and oviposit for 7 days before removal.

No progeny developed in protein-rich feed diets (sunflower meal, soybean concentrate, corn gluten). In two other types of feed diet: carbohydrates-rich feeds (corn feed flour, wheat bran, coarse wheat) and compound feed for pigs and laying hens, first adults required the least time to emerge in wheat bran (15.7-16.5 days) and control diet (wheat flour + 5% yeast) (15.2-16 days), and the longest in corn flour (23.1-24.5 days). In wheat bran and control diets, adult emergence required the shortest period (15.7 and 15.2 days) at the initial population densities of 100 and 50 adults/50g, and significantly longest (16.5 and 16 days) at the lowest density. Conversely, in hens diet adults emerged the latest, after 22.5 days, at the population density of 100 adults/50g, and the earliest, after 18.6 days, at 25 adults/50 g. The shortest period of adult emergence at all population densities was found in the control (15.9-20.2 days) and wheat bran (18-29.7 days), and the longest in compound feed for hens (56.2 days) and pigs (59.5 days) at the highest population density. Considering all densities, number of progeny were the highest in control diet (498-1226 adults) and wheat bran (354-1344 adults), and lowest in coarse wheat (220-300 adults). With increasing population density, progeny body weight decreased, and the highest weight was found in control diet and wheat bran (1.7 and 1.6 mg) at the lowest population density, and the lowest weight (1.0 mg) in hen and pig feeds at the highest density.

Keywords: *T. castaneum*; population density; feed diets; development rate; body mass.

1. Introduction

Global feed production for domestic animals has approached an annual volume of one billion tons, according to reports by the International Feed Industry Federation - IFIF (www.ifif.org) and the current increase in global demand requires steps to be taken towards reducing losses and improving the quality and safety of these products. The quality and safety of plant feeds are considerably threatened by stored-product insect pests, which annually damage 10-20% of the stored products worldwide (Gorham, 1991, Mason and McDonough, 2012).

The red flour beetle *Tribolium castaneum* Herbst is an important pest of stored plant products, especially processed commodities, which makes it one of the most important pests in facilities for manufacturing and storage of plant feeds (Rees, 2004, Mahroof nad Hagstrum, 2012). The type of stored plant products and their nutritive value affect significantly the speed of development and abundance of progeny, and consequently the detriment that *T. castaneum* and other stored-product insects are able to cause (Sokoloff et al., 1966a; Sokoloff et al., 1966b; Baker, 1988; Jagadeesan et al., 2013). Feed industry is mainly focused on plant products rich in carbohydrates (corn and wheat meals) and proteins (soybean, sunflower and a variety of soybean and sunflower products) and compound feed (ready-to-use meals) that may contain vitamins, amino acids, micro- and macro-nutrients (Lević and Sredanović, 2011; Lević et al., 2012; Corrent, 2013, 2015; Laune, 2015; Cerrate, 2015; Liu and Selle, 2015)

T. castaneum has been observed to have a shorter life cycle and greater progeny counts on whole grain flour, while its cycle is considerably longer and number of progeny considerably lower on diet brown and rice flour (Wistrand, 1974). On the other side, cotton seed (Ahamad et al., 2012) and some starch (Wong and Lee, 2011) diets are poor providers for *T. castaneum* progeny. Additives, such as brewer's and baker's yeast, added to different diets have stimulating effects on the developoment cycles and number of progeny of *T. castaneum* (Sokoloff et al., 1966a; Lale et al., 2000). The types of diet or their combination may also significantly affect the body weight of progeny of various stored-product insects

(LeCato, 1976) or pheromones secreted by males of species such as *T. castaneum* (Ming and Lewis, 2010). Apart from the type of diet, initial population density may also have a direct or indirect impact on the reproduction, development rate, number of progeny and body weight of stored-product insects (Taylor, 1974; Longstaff, 1995; Assie, 2008). Depending on the quality of diet, high initial population densities of *T. castaneum* may cause significantly longer life cycles and lower number of progeny (Longstaff, 1995).

Hitherto research has been mainly focused on the occurrence, development and harmfulness of *T. castaneum* in stored products intended for human diet, while information about its harmfulness and development in primary and processed plant products is scarce, despite the high scope of losses caused in feed industry each year. The present study therefore examined the effect of different initial population densities (10, 25, 50 and 100 adults) and substrates as feed diets, namely: a) carbohydrate-rich diets: corn feed flour, wheat bran (wheat feed flour) and coarse wheat meal b) protein-rich diets: corn gluten meal, soybean concentrate and sunflower meal, and c) feed products, i.e. compound feed for fattening pigs and compound feed for laying hens, on several life parameters (first emergence, development rate, number of progeny and body mass of adults) of *T. castaneum* progeny.

2. Material i methods

2.1. Test insects

A laboratory population of *T. castaneum*, reared in an insectary, was used in tests that followed the procedures described by Harein and Soderstrom (1966), and Bry and Davis (1985). The population was reared in 2.5 L glass jars containing white wheat flour with 5% active dry yeast. Air temperature in the insectary was 25 ± 1 ºC, and relative humidity 60 ± 5 %.

2.2. Feed substrates as diets

The following substrates were used as feed diets: 1) carbohydrate-rich plant feed diets: corn feed flour containing 10% proteins and 51% carbohydrates (as labeled by Mirotin Tisa d.o.o, Savino Selo); coarse wheat meal produced by milling whole wheat grain of cv. NS 40S, containing 11% proteins and 73% carbohydrates (as labeled by the Institute for Field and Vegetable Crops, Novi Sad); wheat feed flour – bran with 16% proteins and 60% carbohydrates (as labeled by Letina d.o.o, Novi Bečej); 2) protein-rich plant feed diets: corn gluten meal with 60% proteins (as labeled by Jabuka A.D. Starch Industry, Pančevo), soybean concentrate with 66% proteins (as labeled by Soja Protein, Bečej), sunflower meal containing 33% proteins (as labeled by Letina d.o.o, Novi Bečej), and 3) feed products, i.e. compound feed for fattening pigs, containing: proteins (min 16 %), cellulose (max 8 %), calcium (0.6-0.8 %), phosphorus (min 0.55 %), sodium (0.15-0.25 %), lysine (min 0.8 %), methionine + cysteine (min 0.45 %), vitamins (A, D3), micro- and macro-nutrients (Fe, Mn, Cu, Zn, I, Co, Se) (as labeled by Letina d.o.o, Novi Bečej) and compound feed for laying hens, containing: proteins (min 16.5 %), cellulose (max 8 %), calcium (3.2-4 %), phosphorus (0.65-0.85 %), sodium (0.15-0.2 %), lysine (min 0.75 %), methionine + cysteine (min 0.65 %), vitamins (A, D3, E), micro- and macro-nutrients (Fe, Mn, Cu, Zn, I, Co, Se) (as labeled by Letina d.o.o, Novi Bečej). The control diet was a soft wheat flour type 500 containing supplementary brewer's yeast (5%).

All diets used in this study were sterilized (60°C for 10 h) to eliminate potential insect infestation (Tuncbilek and Kansu, 1996). After sterilization, all substrates were kept at 25±1 °C temperature for 12 h before using them in the experiments.

2.3. Bioassay

The experiment was carried out in the laboratory following the modified methods described by Longstaff (1995). Each type of diet (50 g) was placed into 200 mL plastic containers, separately for each of four population densities (10, 25, 50 and 100 adults) of *T. castaneum*. Unsexed adults aged two to four weeks were then added to each diet/population density combination in four replicates. The containers were covered with cotton cloth, fixed with rubber bands and put in an incubator (Sutjeska, Serbia) set to 30±1°C temperature and 50±5% r.h. The entire procedure was repeated twice. The beetles were allowed to feed and oviposit for 7 days after which period they were gently removed by sieving with minimal distrubance of the developing progeny, and the containers were again put in the incubator. Adult mortality was ≤ 1 % in all trial combinations and all adults discarded.

Detailed checks of all containers began 10 days later in oder to determine the moment of first emergence of F_1 adults and that moment was marked as day 1 for each diet/population density combination. Once the first adult developed, each diet was examined daily, and any new adults were counted and removed. Adult emergance was recorded in each container until the last adult developed. During the count checks, new adults were randomly selected and placed in 200 mL plastic containers with soft wheat flour and left in a room at 25±1ºC temperature and 50±5 % r.h. Ten days later, total body mass of 10 adults was measured on the analytical scale (Denver instrument, USA) and average body weight of F_1 adults calculated. The entire procedure was repeated ten times in the course of the experiment, always with new adults, except for the adults developing in the feed for laying hens at the population density of 100 adults, where the entire procedure was repeated eight times.

The data were calculated to obtain information about the first adult emergence, adult development rates, average total number of progeny and their body weight. In the protein-rich diets, i.e. corn gluten meal, soybean concentrate and sunflower meal, a low number of larvae was detected in daily checks which failed to reach the pupal stage, and they were excluded from further data processing.

2.4. Data analysis

Number of progeny were analyzed by repeated ANOVA processing. The repeated factor was **day of development rate** (examined daily), while number of progeny was the response variable, and the main effects were diet (except for corn gluten meal, soybean concentrate and sunflower meal because no adults emerged) and population density. Before analyses, progeny number in the F_1 generation were transformed using log (x+1). However, the tables show untransformed means and standard errors. A one-way ANOVA was used for comparing: the first emergence of adults, adult development rates, average total number of progeny and their body mass, and the means were separated by Fisher's LSD test at $P < 0.05$ (Sokal and Rohlf, 1995). The data were run on StatSoft version 7.1 (StatSoft Inc., Tulsa, Oklahoma).

3. Results

Both main effects and their associated interaction for number of progeny of *T. castaneum* were significant (diets: $F_{5,168}=17.5$; $P<0.0001$; population density: $F_{3,168}=50.7$; $P<0.0001$; diets x population density: $F_{15,168}=6.3$; $P<0.0001$), as well as the adult development rates: $F_{67,11256}=622.7$; $P<0.0001$; adult development rates x diets: $F_{335,11256}=31.4$; $P<0.0001$; adult development rates x population density: $F_{201,11256}=20.8$; $P<0.0001$; adult development rates x diets x population density: $F_{1005,11256}=6.6$; $P<0.0001$.

3.1. First emergence and development rates of adults

The average number of days between parent removal and the first day of emergence of their progeny (adults) differed significantly per initial population density and type of diet (Table 1). The effects of initial population density on the first day of adult emergence within diet groups was the most evident for the laying hens feed at the highest initial population density (100 adults/50 g diet) as adults started to emerge significantly later, i.e. after 22.5

days, while the earliest emergence occured from the density of 25 adults after 18.6 days. In corn feed flour, first adult emergence at the initial population density of 100 adults required significantly longer duration (24.5 days) than at the initial densities of 25 and 50 adults (23.5 and 23.1 days, respectively). Conversely, the shortest time interval (15.7 and 15.4 days) for adult emergence in the F_1 generation in wheat feed flour (wheat bran) and control diet was found at the highest population density, while the duration was significantly longest (16.5 and 16 days) at the lowest population density. Comparing all investigated diets and population densities, first adult emergence required the shortest time in wheat bran (15.7-16.5 days) and control diet (15.2-16 days), statistically significantly longer in the laying hens diet (18.6-22.5 days), and the longest in corn feed flour diet (23.1-24.5 days).

The initial population density and type of diet had statistically significant effects on the development rate of *T. castaneum* progeny (figure 1-4). For all diets, the lowest development rate (15.9-23.6 days) was found at the lowest initial population density and the highest (20.2-59.5 days) at the highest density (Table 2). Type of diet also had a significant effect on the duration of emergence. The highest adult development rate at all population densities was found in wheat bran (18-29.7 days) and control diet (15.9-20.2 days), while the lowest development rate was found on the compound feed for fattening pigs (59.5 days) and compound feed for laying hens (56.2 days) at the highest initial population density.

3.3. Number of progeny

Total number of progeny varied with statistical significance depending on the initial population density and diet (figure 1-4). With increasing initial population density there was a significant increase in average total number of progeny within diet types, an exceptions being the pig and laying hen feeds where the lowest progeny counts occurred from the highest initial population density (354.7 and 147.1 adults, respectively), and the highest number of progeny from the initial density of 25 insects (773.5 and 645 adults) (Table 3). Considering all population densities, except in the control (498.2-1226.4 adults), the highest number of progeny were generally found in wheat bran (353.7-1344.2 adults), and the lowest in coarse wheat meal (220.1-298.9 adults).

3.4. Body mass of emerged adults

The average body mass of progeny/adults varied significantly compared to the initial population densities and types of diet. The influence of initial population density on progeny body mass was high for each substrate, so that progeny body mass decreased with increasing population density in all diets, and the most significant difference occured in the compound feed for fattening pigs and compound feed for laying hens where body mass of the newly emerged adults was 1.010 mg and 0.994 mg, at the highest population density, and 1.580 and 1.503 mg at the lowest density, respectively (table 4). The highest adult body mass, considering all examined raw and processed feeds for domestic animals, was found in wheat bran (1.625 mg) at the lowest population density (10 adults/50g diet).

4. Discussion

4.1. First emergence and development rates of adults

Initial population density had a significant impact on the first day of progeny emergence only for the compound feed for laying hens as the first day of emergence at the highest initial density was almost 4 days later than it was at the initial density of 25 insects. Comparing all diets, first emergence in corn feed flour occurred the latest (24.5 days) at population density of 100 adults/50 g diet, and it was 1.6-fold slower than it was in the control diet and wheat bran, where the adults appeared first. Longstaff (1995) found the first emergence in soft wheat flour at an initial population density of 9 and 26 pairs of *T. castaneum* to occur 17 and 42 days later than at the initial density of 1 and 3 pairs, while first emergence in hard wheat flour at the highest population density was 2-3 days sooner than it was at the lowest initial population density.

Generally, the adult development rates in all diets at the higher initial population densities were significantly higher than they were at lower initial densities. This finding was especially evident in the compound feed for fattening pigs and compound feed for laying hens, where the development rate at the highest population density was 3.2- and 2.4-fold higher than the rate at the lowest initial density. The quality of diets at all population densities significantly affected the adult development rates. The most significant impact was found at the highest population density, so that the adult development rates were 1.8, 1.5, 2.2, 2.9 and 2.8 times higher in coarse wheat meal, wheat bran, corn feed flour and compound feed for fattening pigs and compound feed for laying hens than in control diet (wheat flour + 5% baker's yeast). Sokoloff et al. (1966a) found that the relative development rates of *T. castaneum* in diets of corn meal, polished rice, soybean and whole wheat flour with yeast additive were 14-28 days shorter than in the same diets without yeast. Faradisi et al. (2013) reported that the larval period significantly extended, 2.4 and 1.8 times, on the diets of DDGS 1 and 2 (maize distillation products used for pig nourishment) compared to control diet (wheat flour 90 % and brewer's yeasts 10 %). Wong and Lee (2011) found that the average development rate in wheat flour, self-rising flour and rice flour was 1.3, 2.6 and 3.8 times higher than in atta flour. On the other side, Longstaff (1995) noted that the adult development rate at the highest population density (26 pairs) was 90 days in soft wheat, and 50 days in hard wheat, while the period lasted 41 and 48 days, respectively, at the lowest density (1 pair). Testing progeny production in several populations of *Sitophilus oryzae* (F.) (20 mixed sex weevils feeding for 7 days at 28 °C), Baker (1988) found that the adult development rate in wheat grain was significantly lower (34.5 days) than it was in maize grain (42.7 days). In our study, the adult development rate was 16.2-29.7 days in whole wheat flour, and 23.6-43.9 days in corn meal.

4.2. Number of progeny

Increasing initial population density coincided with increasing number of progeny, resulting in the average number of adults in control diet, coarse wheat meal, wheat bran and corn feed flour to be 2.5, 1.3, 3.4 and 3.7-fold higher at the highest population density than at the lowest density. In a study similar to ours, Taylor (1974) found that total number of progeny of *Callosobruchus maculatus* (F.) females in progeny at the population density of 40 adults (20 males and 20 females) fed on a diet of 100 g cowpea was 2.8-fold higher than it was at the density of 10 adults (5 males and 5 females), and 1.6-fold higher at the same densities when the diet was 150 g of cowpea. However, 1.3 and 2.9-fold lower number of progeny were found in our compound feed for fattening pigs and compound feed for laying hens at the highest population density than at the lowest density. This may be partially due to canibalism, i.e. an increased competition among insects as a result of insufficient nutritive supplies (Wistrand, 1974) as we found canibalized pupa, as well as a large number of canibalized larvae, on all substrates, but mostly in the compound feeds. Longstaff (1995) made a similar report and attributed canibalism to larvae because adults were seaved out after a week in a procedure identical to ours. Alabi et al. (2008) found a potential benefit from larval canibalism in its increasing the chances for survival and reaching the adult stage, as well as in shorter life cycle and greater body weight at the adult stage.

The nutritive value of substrates had a significant effect on total number of progeny. In the protein-rich feeds, i.e. sunflower meal (33%), corn gluten (60%) and soybean concentrate (68%), *T. castaneum* failed to develop any progeny, except only a few larvae that died before reaching the pupal stage. Soybean products, including soybean concentrate, contain various antinutritive components, including substances inhibiting the protein trypsin, which is why soybean flour and the inhibitor were found to have a weak insecticidal effect on the pest (Tamgno and Tinkeu, 2014). The isolated soybean inhibitor trypsin in a combination with the potato inhibitor cystein had a negative effect on larval development of *T. castaneum* (Oppert, et al., 2003). Conversely, Sokoloff et al. (1966a) found a significant number (417) of *T. castaneum* adults in the progeny on soybean flour, but 1.9 and 2.6 times higher counts were found in whole wheat flour and corn flour. Contrary to our findings, Wong and Lee (2011) reported 462 progeny adults of *T. castaneum* in atta flour diet (12.8 % protein and 80.8 % carbohydrate), while no progeny was found in corn flour (0.17 % protein and 99.6 % carbohydrate). In raw plant feeds with high contents of carbohydrates, the highest number of progeny at all population densities were found in wheat bran (60 % carbohydrate, 16 % protein), which was 2 and 4.1-fold higher at the density of 100 adults per replicate than it was in corn feed flour (51 % carbohydrate) and coarse wheat meal (73 % carbohydrate). Studying the species *Cryptolestes ferrugineus* (Stephens), Jagadeesan et al. (2013) found 1.3 and 3.8 time higher counts in wheat flour than in maize flour and cracked wheat. Progeny counts of *S. oryzae* in wheat grain were 2.6-fold higher than in maize grain (Baker,1988). Comparing all examined substrates, the highest progeny counts were found in wheat bran (353.7-1344.2 adults), and the lowest in coarse wheat meal (220.1-300.1 adults) even though the two diets are similar in their nutritive value because all wheat grain components are processed (endosperm, aleurone and germ). We assume that the reason for this is most probably the size and structure of substrate particles because coarse wheat grain particles are considerably larger and rougher than those of wheat bran. Earlier studies had shown that the species *T. castaneum* prefered smaller and finer particle size and that female fertility was greater and adult development rate lower in substrates with finer particle structure (Faradisi et al., 2013, Li and Arbogast, 1991).

Number of progeny in wheat bran were similar to the control diet. The white wheat flour used for the control diet consists of grain endosperm, while the feed-grade wheat flour consists of endosperm, as well as aleurone and germ, which makes it richer in energy and far more nutritive than flour (Rosenfelder et al, 2013; Apprich et al., 2014; Kraler et al., 2014). However, the control diet included also 5 % of brewer's yeast, which is known to stimulate progeny production and other life parametars of *T. castaneum* (Sokoloff et al., 1966a; Lale et al., 2000).

In the compound feed for fattening pigs and compound feed for laying hens that contain proteins, but also vitamins, amino acids, micro- and macro-nutrients (Corrent, 2015; Laune, 2015) high number of progeny were found at the lowest population density, which indicates high nutritive values of those diets, while the highest population density caused insufficient food supply for the many larvae, which resulted in competition and canibalism, and ultimately in low number of adult progeny.

4.3. Body mass of emerged adults

Population density affected the adult body weight of beetles in all diets, and that influence was more or less evident depending on the nutritive value of each diet. The most significant difference was detected in the compound feed for fattening pigs and compound feed for laying hens where the adult body mass at the highest initial population density was 1.6 and 1.5-fold lower than adult body mass at the lowest population density. On the other side, the most significant difference in progeny body mass, considering all diets, was detected at the highest population density, so that adults in the control diet had 1.6 times higher body mass than those in the feeds for pigs and hens. LeCato (1976) also reported a significant effects of diet quality on the body mass of newly-emerged adults while testing the effects of 21 types of diets on the body mass of adults of *Candra cautella* (Walker) and *Plodia interpunctella* (Hubner). Compared to control diet, the body mass of *C. cautella* and *P. interpunctella* adults in corn meal and wheat meal was 1.2 and 2.5, and 1.6 and 3.9-fold lower. A recent study (Assie et al., 2008) showed that females from populations with lower initial densities had around 10% greater body mass than females from populations with higher initial densities.

5. Conclusion

We inferred from the data in our present study that initial population density and type/nutritive value of feed diets have significant effects on the life parameters of *T. castaneum:* first emergence, development rate, number of progeny and body mass of progeny. Also, the brief life cycle at the lowest population densities and 30 °C temperature suggests that the summer season is critical for feed storage. The results of the present study make a valuable contribution to expanding the knowledge about the life parameters of that pest species, optimal storage time and feed protection from this one and other stored-product pests.

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Table 1. First emergence of *T. castaneum* adults at different population densities and feed diets

Feed diet	First adult emergence (days) (x ± SE)			
	Initial population density (No./50 g of diet)			
	10	25	50	100
Control[*]	16.0 ± 0.0Da[**]	15.6 ±0.3Dab	15.2 ± 0.2Db	15.4 ± 0.2Eb
Coarse wheat meal	19.5 ±0.4Ba	19.0 ±0.4Ba	19.7 ± 0.6Ba	19.7 ±0 .4Ca
Wheat bran	16.5 ±0.3Da	16.2 ± 0.2Dab	16.1 ± 0.2Dab	15.7 ± 0.2Eb
Corn feed flour	23.5 ±0.3Aab	23.1 ± 0.2Ab	23.7 ± 0.4Aab	24.5 ± 0.5Aa
Compound feed for fattening pigs	17.7 ± 0.4Ca	17.2 ± 0.2Ca	17.4 ± 0.3Ca	17.6 ± 0.2Da
Compound feed for laying hen	19.2 ± 0.3Bb	18.6 ± 0.2Bb	19.9 ± 0.5Bb	22.5 ± 1.4Ba

[*] Wheat flour + 5% yeast[*]

[**] Means within columns followed by the same uppercase letter and mean within rows followed by the same lowercase letter are not significantly different, Fisher's LSD test at P < 0.05

Table 2. Adult development rates of *T. castaneum* at different population densities and feed diets

Feed diet	Adult development rate (days) (x ± SE)			
	Initial population density (No./50 g of diets)			
	10	25	50	100
Control[*]	15.9 ± 0.3Cc[**]	18.6 ± 0.5Db	19.0 ± 0.5Cab	20.2 ± 0.4Da
Coarse wheat meal	17.2 ± 0.8BCc	21.1 ± 0.7CDbc	26.1 ± 2.0Cb	35.9± 4.2Ca
Wheat bran	18.0 ± 0.6Bd	20.9 ± 0.2CDc	24.1 ± 0.5Cb	29.7 ± 1.2Ca
Corn feed flour	23.6 ± 0.5Ac	33.2 ± 0.6Ab	36.5 ± 1.1Bb	43.9 ± 2.3Ba
Compound feed for fattening pigs	18.7 ± 0.5Bc	25.9 ± 0.5BCc	42.0 ± 6.3ABb	59.5 ± 2.1Aa
Compound feed for laying hen	23.1 ± 1.1Ab	32.2 ± 5.3ABb	51.1 ± 4.7Aa	56.2 ± 2.3Aa

[*] Wheat flour + 5% yeast[*]

[**] Means within columns followed by the same uppercase letter and mean within rows followed by the same lowercase letter are not significantly different, Fisher's LSD test at P < 0.05

Table 3. Average total number of progeny of *T. castaneum* at different population densities and feed diets

Feed diet	Average total number of progeny (x ±SE)			
	Initial density (No./50 g of diets)			
	10	25	50	100
Control*	498.2 ± 39.2Ac**	929.2 ± 46.6Ab	1129.4 ± 36.6Ba	1226.4 ± 46.7Aa
Coarse wheat meal	220.1 ± 25.4Cb	260.0 ± 2 4.2Dab	300.1 ± 16.8Da	298.9 ± 18.9CDa
Wheat bran	353.7 ± 55.4Bc	848.2 ± 43.7ABb	1344.2 ± 34.1Aa	1221.5 ± 58.8Aa
Corn feed flour	163.6 ± 13.3Cd	349.1 ± 13.6Dc	418.5 ± 18.4Db	602.4 ± 24.6Ba
Compound feed for fattening pigs	466.9 ± 39.7ABb	773.5 ± 0.1Ba	757.4 ± 76.7Ca	354.7 ± 90.4Cb
Compound feed for laying hen	432.6 ± 63.5ABa	645.0 ± 63.0Ca	469.7 ± 110.6Da	147.1 ± 60.5Db

[*] Wheat flour + 5% yeast*

[**] Means within columns followed by the same uppercase letter and mean within rows followed by the same lowercase letter are not significantly different, Fisher's LSD test at $P < 0.05$

Table 4. Adult body weight of *T. castaneum* at different population densities and feed diets

Feed diet	Adult body weight (mg) (x ±SE)			
	Initial density (No./50 g of diets)			
	10	25	50	100
Control*	1.722±0.014Aa**	1.724±0.021Aa	1.671±0.037Aa	1.599±0.020Ab
Coarse wheat meal	1.547±0.015BCDa	1.473±0.024BCb	1.407±0.012Cc	1.320±0.016Bd
Wheat bran	1.625±0.046Ba	1.542±0.025Bab	1.512±0.033Bb	1.389±0.041Bc
Corn feed flour	1.478±0.020Da	1.415±0.034CDab	1.348±0.041Cbc	1.303±0.048Bc
Compound feed for fattening pigs	1.580±0.036BCa	1.493±0.026BCa	1.535±0.006Ba	1.010±0.043Cb
Compound feed for laying hen	1.503±0.025CDa	1.387±0.039Da	1.244±0.048Db	0.994±0.067Cc

[*] Wheat flour + 5% yeast*

[**] Means within columns followed by the same uppercase letter and mean within rows followed by the same lowercase letter are not significantly different, Fisher's LSD test at $P < 0.05$