Does interspecific competition between *Tribolium castaneum* and *Tribolium confusum* lead to thermal habitat segregation?

Honours research project

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Abstract

Interspecific competition can occur when many species are present in the same habitat, and some species can have an effect on other species abundance or distribution. For example, ectotherm distribution depends on temperature, and some species may not be able to achieve their preferred temperature because of interspecific competition. I studied interspecific competition between two flour beetles, *Tribolium castaneum* and *Tribolium confusum*. I used three temperatures based on each species preferred temperature, as well as an intermediate temperature which overlaps both preferred temperatures. I also used 5 treatments with different ratios of *T. castaneum* to *T. confusum*: 1:0, 2:1, 1:1. 1:2 and 0:1. Since many studies have shown that *T. castaneum* appears dominant over *T. confusum* and since both species have distinct preferred temperatures, I tested the hypothesis that the distribution of *T. castaneum* and that of *T. confusum* should be a function of temperature and a function of the relative abundance of the two species. I also tested the hypothesis that the population growth rate of each species should be a function of the relative abundance of the two species. Both species showed a preference for the cool habitat at the beginning of the experiment when density was low, and both species changed their preference for the warm habitat as density increased. Also, *T. castaneum* and *T. confusum* abundance did differ between treatments, but the presence of one species did not affect the other species final population size, and the final population size did not differ between the species for the two-species treatments. These results do not match my predictions that competition would occur as *T. castaneum* is normally dominant over *T. confusum*.

Introduction

Interspecific competition is an important driver of the distribution of organisms. When many species are present in the same habitat, competition is higher, which may cause each species to be less abundant (Kolbe et al., 2008; Sato et al., 2014). For instance, Morris et al. (2000) studied interspecific competition between two lemming species and showed that *Lemmus trimucronatus* presence had a negative impact on *Dicrostonyx groenlandicus*: the density was reduced in its preferred habitat. However, the reverse was not observed: *L. trimucronatus* density was not affected by *D. groenlandicus* presence. Hodara et al. (2000) also showed that the density of a species can be affected by competition in two rodent species. *Calomys laucha* was found mostly in crop fields because of its competitor presence in the edges. They suggested, however, that when resources were getting lower, *C. laucha* was present more often in the edges.

Temperature is a crucial environmental factor for ectotherms. Ectotherms have a tolerance zone of temperature in which they can live, as well as an optimal range of temperatures in which they perform best (Huey & Kingsolver, 1989; Magnuson et al., 1979). The distribution of ectotherms across a range of temperatures can be affected by the presence of other species. For example, Magnuson et al. (1979) showed that one fish species was more present in cold water than in warm water in the presence of a competitor. Moreover, Kolbe et al. (2008) studied spatial distribution between lizards and showed that *Anolis wattsi* was found most of the time in sunny areas on an island. However, on another island where *Ameiva griswoldi* was present, *A. wattis* was rarely present in these sunny habitats.

I studied interspecific competition between *Tribolium castaneum* and *Tribolium confusum*. Several studies have shown that these species have different thermal preference and development rate that can affect the outcome of competition. For example, *T. castaneum* prefers a temperature

of 34°C for pupation, compared to 30°C for *T. confusum* (King & Dawson, 1973). Park and Frank (1948) mention that *T. castaneum* may have an advantage over *T. confusum* at higher temperatures, while *T. confusum* may have this advantage at lower temperatures. Some studies found that *T. castaneum* may be a better competitor than *T. confusm*. Park & Frank (1948) found that *T. castaneum* laid more eggs than *T. confusum* at all temperatures tested: 24, 29, and 34°C. The adults of both species eat more *T. confusum* eggs than *T. castaneum* eggs (Park et al., 1965; Teleky, 1980). Also, *T. castaneum* adults are more cannibalistic than *T. confusum* adults (Teleky, 1980), and Lavie (1980) demonstrated that *T. castaneum* dominated *T. confusum*. Finally, temperature can affect the duration of the different life stages (Howe, 1956; Howe, 1960) and since the development time of *T. confusum* is longer than that of *T. castaneum* (Goodnight & Craig, 1996; Howe, 1960; Lavie, 1980; Park & Frank, 1948), there is more chance for *T. confusum* to be exposed to cannibalism, since the pupal stage will be longer (Goodnight & Craig, 1996).

I tested the general hypothesis that the distribution of *T. castaneum* and that of *T. confusum* should be a function of temperature and a function of the relative abundance of the two species. I used three temperatures because 23°C is preferred by *T. confusum* and 32°C is preferred by *T. castaneum*, while 28°C is a zone of preference overlap for the two species (Fig. 1; Halliday & Blouin-Demers, 2015). I also used treatments with different ratios of each species (1:0, 2:1, 1:1, 1:2, and 0:1). Because *T. castaneum* and *T. confusum* have distinct preferred temperatures, I tested the prediction that the distribution of *T. castaneum* should be biased towards warmer habitats and the distribution of *T. confusum* should be biased towards cooler habitats. Because *T. castaneum* appears dominant over *T. confusum*, I also tested the prediction that *T. confusum* should be increasingly confined to cool temperatures as the density of its competitor, *T.*

castaneum, increases. I also tested the hypothesis that the population growth rate of each species should be a function of the relative abundance of the two species. Because *T. castaneum* is the dominant species, I tested the prediction that the population growth rate of *T. castaneum* should be higher in the two-species treatments. Therefore, *T. castaneum* should eventually become more abundant than *T. confusum* even if *T. confusum* was the most abundant at the beginning of the experiement.

Materials and Methods

I studied two species of flour beetles, *T. castaneum* and *T. confusum*. The beetles originally came from Carolina Biological Supply Company (Burlington, North Carolina, USA). There were 200 individuals of each species at the beginning, and the colonies were grown to around 5000 beetles. The colonies were kept in an incubator at 30°C, 70% relative humidity with a cycle of 12 hours of dark and 12 hours of light for 2.5 years prior to the experiment. I kept cultures in containers filled with a mixture of 95% wheat flour and 5% brewer's yeast (henceforth referred to as flour). I used 500 hundred individuals of each species for my experiments.

I started the experiment with five treatments. At the beginning, each treatment was composed of 20 adults, with different ratios of *T. castaneum* to *T. confusum*: 1:0, 2:1, 1:1, 1:2, and 0:1. For the ratios 1:2 and 2:1, I used 13 beetles of a species, and 7 beetles of the other species. I used 10 replicates per treatment, for a total of 50 replicates. Each replicate was conducted in containers with three temperatures (23°C, 28°C and 32°C), where a third of each container was set at each temperature. I placed heat tapes under the containers to maintain the temperatures. I added 1 cm of sand as a substrate in each container, and I placed a food patch at each temperature of each container. The food patch was two glass slides taped together and placed on the sand, with 2.5 ml

of flour placed on the slides. For treatments with two species, I painted the backs of all individuals with acrylic paint of two colours to distinguish between the species.

I counted the number of adults of each species located in each temperature zone for each replicate once per week. I identified any unpainted new individuals in the treatments with two species based on the shape of their antennae (Good, 1936), and painted them to identify them in future weeks. All the individuals were then put back in the containers in the temperature that I found them in. I also replenished the flour in each food patch every week.

I collected data for this experiment over 15 weeks to measure the abundance and distribution of each species as the populations grew and individuals dispersed between habitats. For the first 7 weeks, I collected data once per week. From the eighth week onwards, I collected data every two weeks, and from the twelfth week onwards, I collected data for 6 of the 10 replicates for each of the treatments 2:1, 1:2 and 1:1; the six replicates were chosen randomly.

I examined the habitat selection of each species in each treatment (1:0, 2:1, 1:1, 1:2, and 0:1), at each temperature (23°C, 28°C and 32°C), and in different periods of population growth (weeks 1 to 4, 5 to 10 and 11 to 15) using ANOVA in R (package: stats; function: aov; R Core Team 2014). I included the two-way interactions between temperature and treatment, and temperature and period. I also used Tukey's Honest Significant Difference test (package: stats; function: TukeyHSD; R Core Team 2014) as a post-hoc multiple comparison test. I included the different periods of population growth to control for changing population size throughout the study. Weeks 1 to 4 represent a period of no growth before new adults emerged, weeks 5 to 10 represent the steepest population growth, and weeks 11 to 15 represent declining population growth.

To determine if increased interspecific competition caused changes in final population size, I examined if the final population size of each species was affected by the population size of the competing species in each treatment (1:0, 2:1, 1:1, 1:2, and 0:1) using ANCOVA in R (package: stats; function: lm; R Core Team 2014). I log-transformed final population size of each species to meet the assumption of normality. I calculated the final population size of each species as the number of individuals of each species in each container on the last week of data collection.

To determine if species differed in their final population size, I compared the final population size of each species in each treatment (1:0, 2:1, 1:1, 1:2, and 0:1) using ANOVA in R (package: stats; function: aov; R Core Team 2014). I used Tukey's Honest Significant Difference test (package: stats; function: TukeyHSD; R Core Team 2014) as a post-hoc multiple comparison test.

For all analyses, I used an automated stepwise process to select the model with the lowest Akaike's Information Criterion (AIC) (package: stats; function: stepAIC; R Core Team 2014). I examined the parametric assumptions of linearity, normality and homoscedasticity of the residuals for each analysis to ensure they were met.

Results

The distribution of *T. castaneum* was affected by two interactions. *T. castaneum* distribution was affected by the interaction between temperature and treatment ($F_{6, 1227} = 3.53$, $p < 0.01$). The interaction was caused by a thermal preference in treatments 2:1 and 1:2, but no thermal preference in the other treatments (Table 1, Figure 2). *T. castaneum* distribution was also affected by the interaction between temperature and time period ($F_{4, 1227} = 88.21$, $p < 0.01$). The interaction was caused by a difference in thermal preference during the time periods. *T.*

castaneum preferred colder temperatures at the beginning of the experiment, but preferred higher temperatures at the end of the experiment (Table 1, Figure 3).

The distribution of *T. confusum* was also affected by interactions. *T. confusum* distribution was affected by the interaction between temperature and treatment ($F_{6, 1224} = 2.83$, $p < 0.01$). The interaction was caused by a thermal preference in treatments 2:1, 1:1 and 1:2, but no thermal preference in the other treatments (Table 2, Figure 4). *T. confusum* distribution was also affected by the interaction between temperature and time period ($F_{4, 1224} = 58.17$, $p < 0.01$). The interaction was caused by a difference in thermal preference during the time periods. *T. confusum* preferred colder temperatures at the beginning of the experiment, but preferred higher temperatures at the end of the experiment (Table 2, Figure 5).

The final population size of *T. castaneum* was unaffected by the final population size of *T. confusum* because the difference in the slope of *T. castaneum* abundance as a function of *T. confusum* abundance was zero (difference = 0, $t = 4.59$, $p < 0.01$). *T. castaneum* abundance did differ between treatments with large starting density differences; *T. castaneum* abundance was higher in the treatments where its starting density was higher. However, its abundance did not differ between the treatments where there were small differences in the starting densities (Table 3, Figure 6).

The final population size of *T. confusum* was not affected by the final population size of *T. castaneum* because the difference in the slope of *T. confusum* abundance as a function of *T. castaneum* abundance was zero (difference = 0, $t = 4.09$, $p < 0.01$). *T. confusum* abundance did differ between most treatments; *T. confusum* abundance was higher in the treatments where its

starting density was higher. However, its abundance did not differ between treatments 2:1 and 1:1, or between treatments 1:2 and 0:1 (Table 4, Figure 6).

To see if the species differed in their population size, I examined the final population size of each species in each treatment. The final population size was not affected by the treatment ($F_{2, 30} = 2.25$, $p = 0.12$), by the species ($F_{1, 30} = 0.14$, $p = 0.71$), or by the interaction between treatment and species ($F_{2, 30} = 2.91$, $p = 0.07$; Table 5, Figure 6).

Discussion

I tested the prediction that the distribution of *T. castaneum* should be biased towards warmer habitats and the distribution of *T. confusum* should be biased towards cooler habitats, based on the results of Halliday and Blouin-Demers (2015). I also tested the prediction that increased interspecific competition would lead to both species being increasingly segregated into the warm (*T. castaneum*) and cool habitats (*T. confusum*). Both species showed a preference for the cool habitat early in the experiment (at low density), but increased preference for the warmer habitats as the experiment progressed (and density increased). This change between the time periods could possibly mean that the habitat preference of adult beetles is affected by population size (i.e. density-dependent habitat selection), growth rate, or by the presence of different life stages (i.e. egg, larva, pupa). For both species, the preferred thermal habitat changed from cold when the population growth rate was zero and the density was low, to warm when the population growth rate was positive and the density was high. These results agree with my prediction for *T. castaneum*, but not for *T. confusum*. Both species also changed their habitat preference under increased interspecific competition, but again, not in the direction that I predicted.

I only counted adult beetles, yet there could have been a lot of important variation in the other life stages. For example, several other studies show that the oviposition rate of *T. castaneum* (Halliday & Blouin-Demers, 2014; Halliday et al., 2015), or both *T. castaneum* and *T. confusum* (Park & Frank, 1948; Halliday & Blouin-Demers, 2015) increases with increasing temperature. Other studies, however, show a decrease in oviposition rate as density increases (Halliday & Blouin-Demers, 2014; Halliday et al., 2015). Both species preferred higher temperatures when the population growth rate was positive. This may be because the beetles were present at the warmer temperatures for ovipositing, which explains the large number of beetles of each species counted at the highest temperatures. For example, Halliday and Blouin-Demers (2015) demonstrated that the optimal temperature for oviposition for both species was around 30°C, which is an intermediate temperature between my medium and hot thermal habitats.

I also tested the prediction that *T. castaneum* would have a higher growth rate than *T. confusum* in the two-species treatments. Both species abundance differed between some treatments. These differences were between 162 and 417 beetles, and the replicates had between 65 and 868 beetles on the last week of data collection. Therefore, we can say that these differences are biologically significant. However, the presence of *T. castaneum* did not affect the final population size of *T. confusum* and vice versa, and the final population size did not differ between both species in the two-species treatments. These results are therefore opposite to my prediction. I found no effect of interspecific competition between the two species, whereas I predicted that *T. castaneum* would be dominant over *T. confusum*.

Several factors may explain these results. Some of the studies looking at competition between the two species only used one temperature (Goodnight & Craig, 1996; Lavie, 1980; Teleky, 1980). Park and Frank (1948) used different temperatures, but they were tested separately. The

fact that the beetles could easily move between three temperatures in my study may have affected the growth rate, and the competition outcome. However, King and Dawson (1973) did a habitat selection experiment with both species combining different temperatures. But they had a more complex system because more temperatures and types of flour were used. They did, however, find that adults had a preferred habitat because individuals were returning to the same cell even after being moved to another one. In the present experiment, the decline in the population growth at the end of the experiment demonstrates that competition started to occur, and it may have been intraspecific competition or interspecific competition. The lack of effect of the final population size of one species on the final population size of the other species leads me to believe that it was intraspecific competition.

Conclusion

In the absence of an interspecific competitor, both species preferred the cool habitat at the beginning of the experiment, and switched preference to the warm habitats as the experiment progressed. With interspecific competition, however, both species shifted their habitat preference more towards the warmer habitats. The final population size of each species did differ between treatments, but the presence of one species did not affect the other's species final population, and the final population size did not differ between the species for the two-species treatments, showing no competition. The fact that I only counted the adults may have made a difference in the thermal habitat results; the same study could be done considering the other life stages of the beetles.

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Table 1. Summary of the final model of *T. castaneum* habitat selection at different temperatures (23°C, 28°C and 32°C), different species ratio of *T. castaneum* to *T. confusum* (1:0, 2:1, 1:1 and 1:2) and different time periods (weeks 1 to 4, 5 to 10 and 11 to 15). The degrees of freedom, the sum of squares, the mean square, the F value and the p value are presented.

T. castaneum

	Df	**Sum sq**	**Mean sq**	*F*	*p*
Temperature	2.00	0.53	0.27	13.20	< 0.01 ***
Treatment	3.00	0	0	0	1
Period	2.00	0	0	0	1
Temperature : Treatment	6.00	0.43	0.07	3.53	< 0.01 **
Temperature : Period	4	7.12	1.78	88.21	< 0.01 ***
Residuals	1227	24.77	0.02		

Table 2. Summary of the final model of *T. confusum* habitat selection at different temperatures (23°C, 28°C and 32°C), different species ratio of *T. castaneum* to *T. confusum* (2:1, 1:1, 1:2 and 0:1) and different time periods (weeks 1 to 4, 5 to 10 and 11 to 15). The degrees of freedom, the sum of squares, the mean square, the F value and the p value are presented.

T. confusum	Df	Sum sq	Mean sq	*F*	*p*
Temperature	2.00	1.53	0.77	40.85	< 0.01 ***
Treatment	3.00	0	0	0	1
Period	2.00	0	0	0	1
Temperature:Treatment	6.00	0.32	0.05	2.83	< 0.01 **
Temperature:Period	4	4.37	1.09	58.17	< 0.01 ***
Residuals	1224	22.98	0.02		

Table 3. Summary of the final model of *T. castaneum* final population size compared to *T. confusum* final population size for different species ratio of *T. castaneum* to *T. confusum* (1:0, 2:1, 1:1, and 1:2) on the last week of data collection. Only the data collected on the 6 replicates for the last weeks have been analysed for treatments 2:1, 1:2 and 1:1. The estimate, the standard error, the t value and the p value are presented. The intercept represents the treatment 1:0.
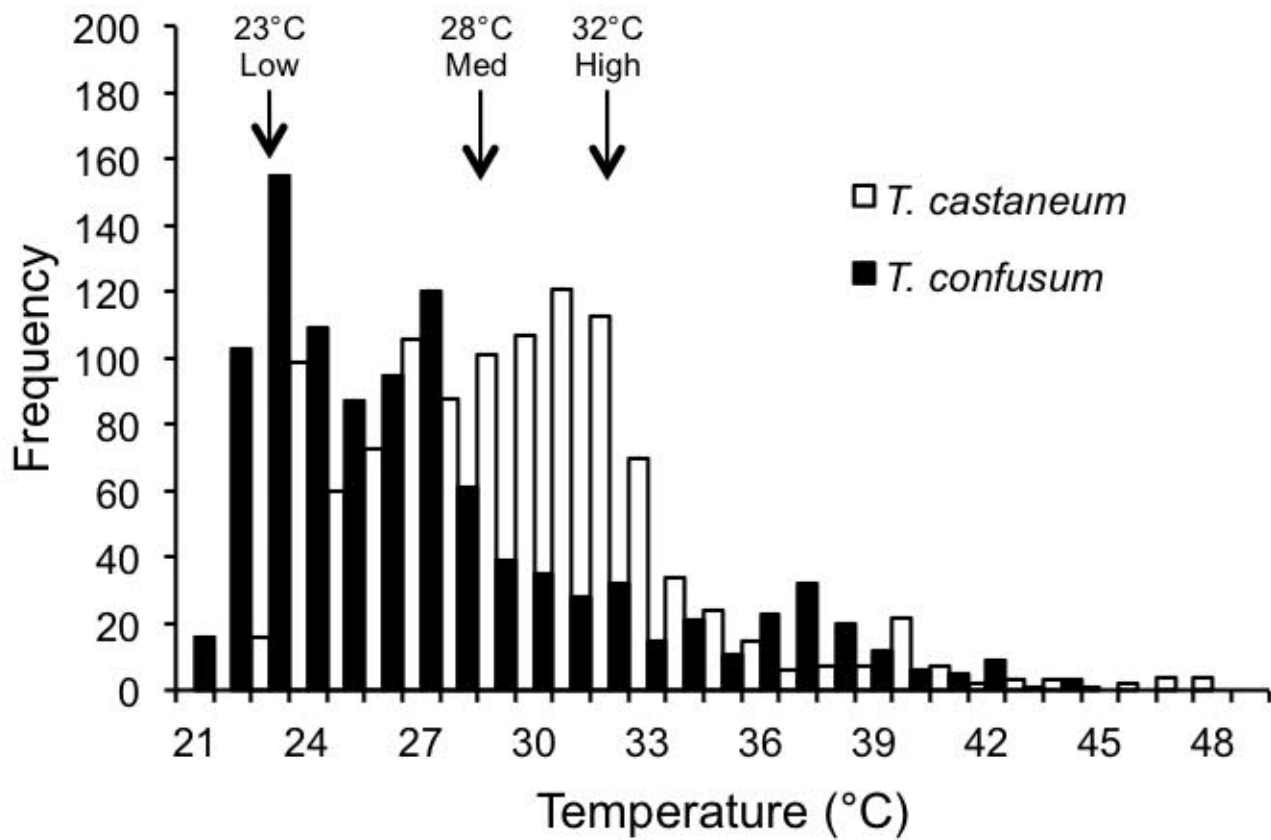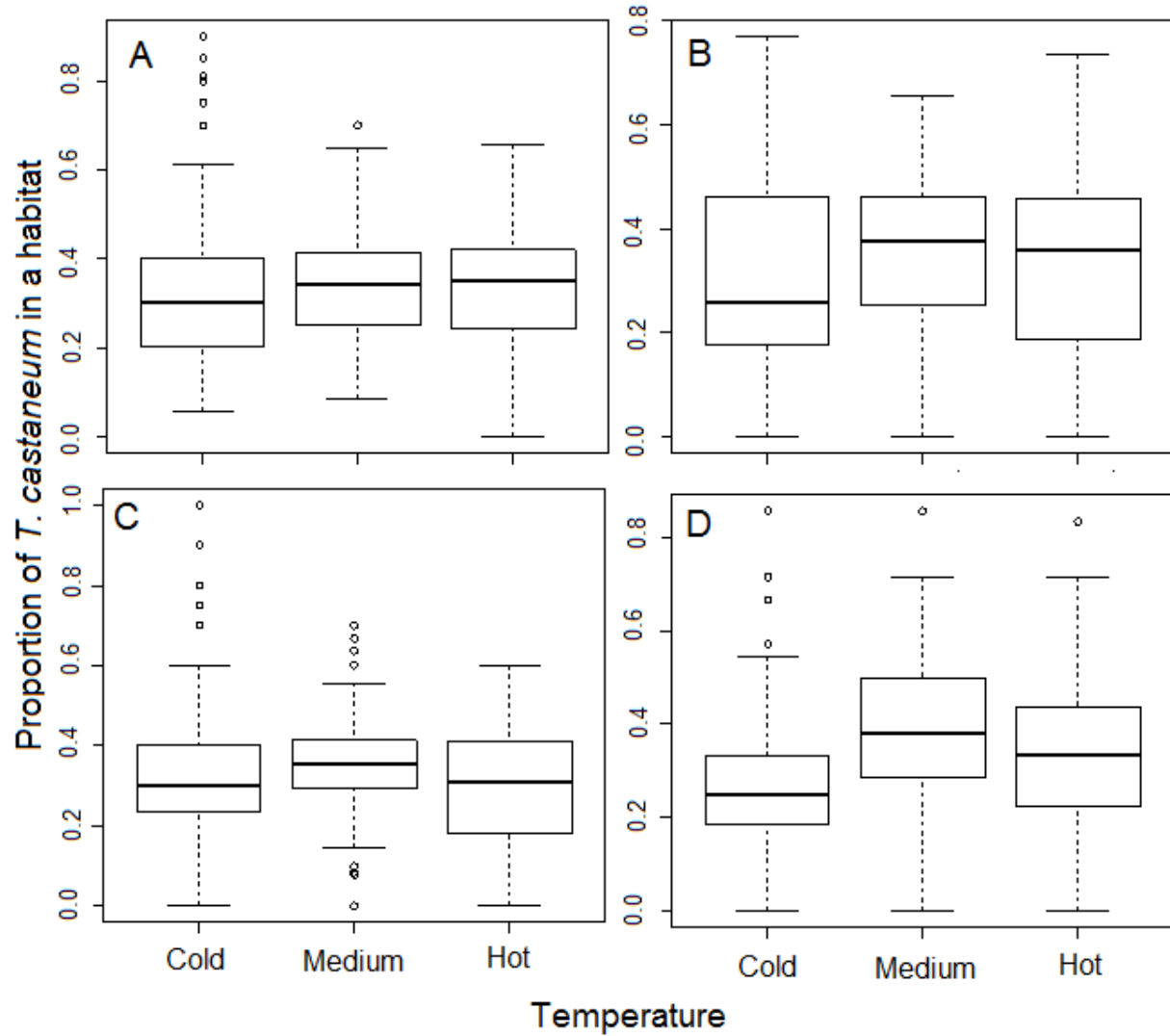
T.castaneum				
	Estimate	**Standard Error**	*t*	*p*
(Intercept)	5.63	0.15	38.05	< 0.01 ***
Treatment 2:1	-0.74	0.33	-2.24	0.04 *
Treatment 1:1	-1.19	0.30	-4.00	< 0.01 ***
Treatment 1:2	-1.74	0.40	-4.30	< 0.01 ***
T. confusum	0.00	0.00	4.59	< 0.01 ***

Table 4. Summary of the final model of *T. confusum* final population size compared to *T. castaneum* final population size for different species ratio of *T. castaneum* to *T. confusum* (2:1, 1:1, 1:2 and 0:1) on the last week of data collection. Only the data collected on the 6 replicates for the last weeks have been analysed for treatments 2:1, 1:2 and 1:1. The estimate, the standard error, the t value and the p value are presented. The intercept represents the treatment 2:1.

T.confusum				
	Estimate	**Standard Error**	*t*	*p*
(Intercept)	3.55	0.52	6.76	< 0.01 ***
Treatment 1:1	0.32	0.39	0.83	0.42
Treatment 1:2	1.04	0.39	2.71	0.01 *
Treatment 0:1	1.81	0.56	3.25	< 0.01 **
T. castaneum	0.00	0.00	4.09	< 0.01 ***

Table 5. Summary of the final model of the final population size for the two-species ratio of *T. castaneum* to *T. confusum* (2:1, 1:1 and 1:2) and for species *T. castaneum* and *T. confusum* on the last week of data collection. Only the data collected on the 6 replicates for the last weeks have been analysed. The degrees of freedom, the sum of squares, the mean square, the F value and the p value are presented.

|	Df	Sum sq	Mean sq	*F*	*p*
Treatment	2	79945	39973	2.25	0.12
Species	1	2483	2483	0.14	0.71
Treatment : Species	2	103589	51794	2.91	0.07
Residuals	30	533478	17783		

Figure 1. Frequency of presence of *T. castaneum* and *T. confusum* at different temperatures, tested by Halliday and Blouin-Demers (2015). The arrows indicate the three temperatures used in the current experiment, one preferred by *T. castaneum*, one preferred by *T. confusum*, and an intermediate temperature.

Figure 2. Proportion of *T. castaneum* in a habitat at different species-ratio and temperatures. For the temperatures, cold=23°C, medium=28°C and hot=32°C. For the species ratio of *T. castaneum* to *T. confusum*, A=1:0, B=2:1, C=1:1 and D=1:2.
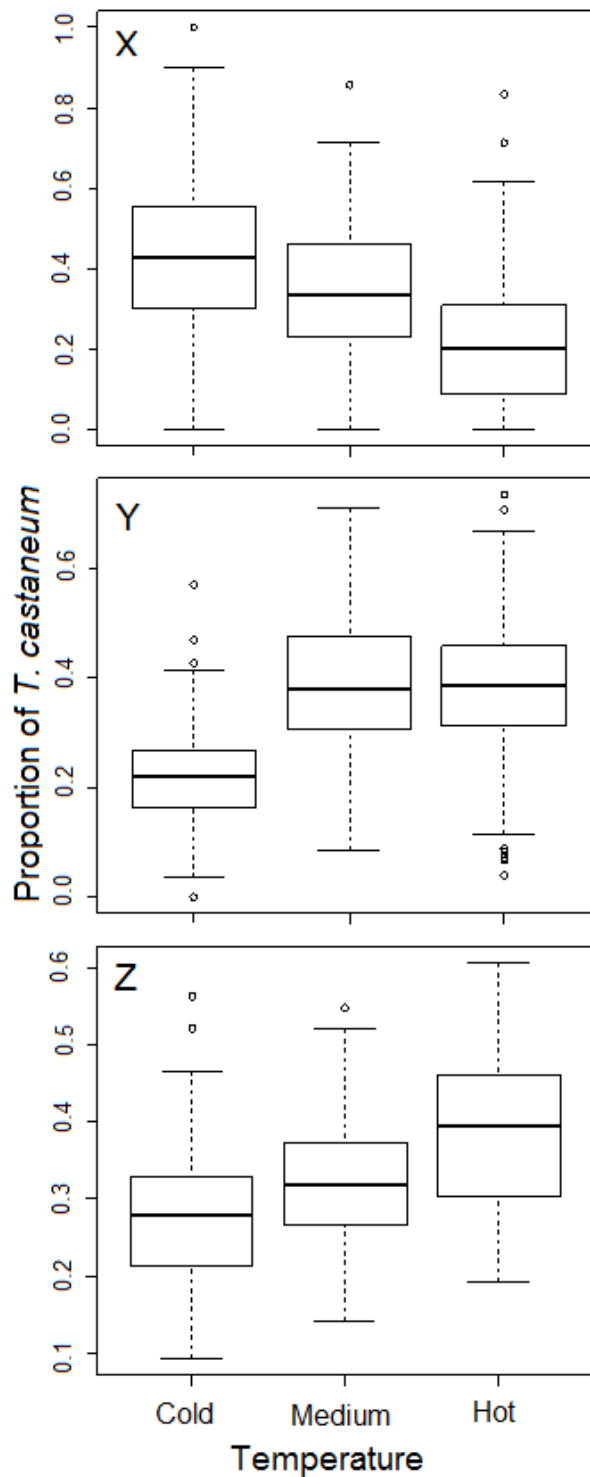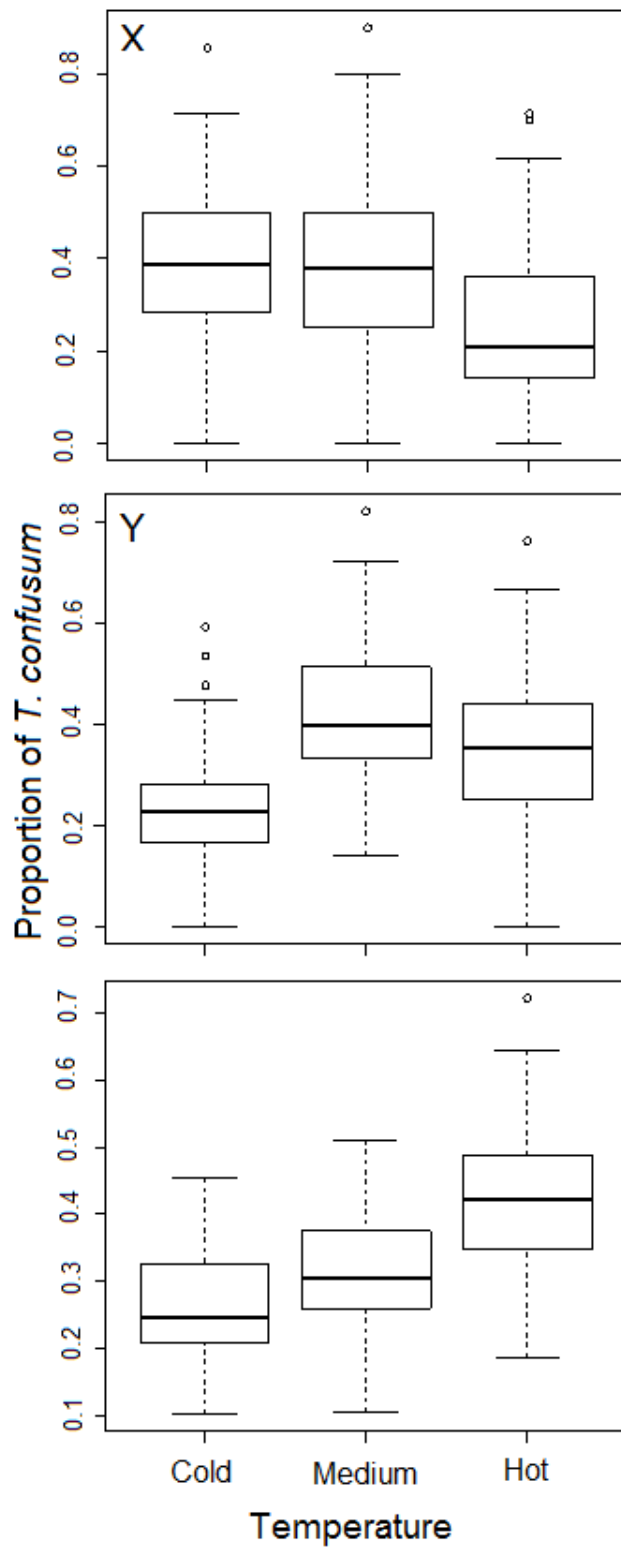
Figure 3. Proportion of *T. castaneum* at different periods and temperatures. For the temperatures, cold=23°C, medium=28°C and hot=32°C. For the periods, X=weeks 1 to 4, Y=weeks 5 to 10 and Z=weeks 11 to 15.
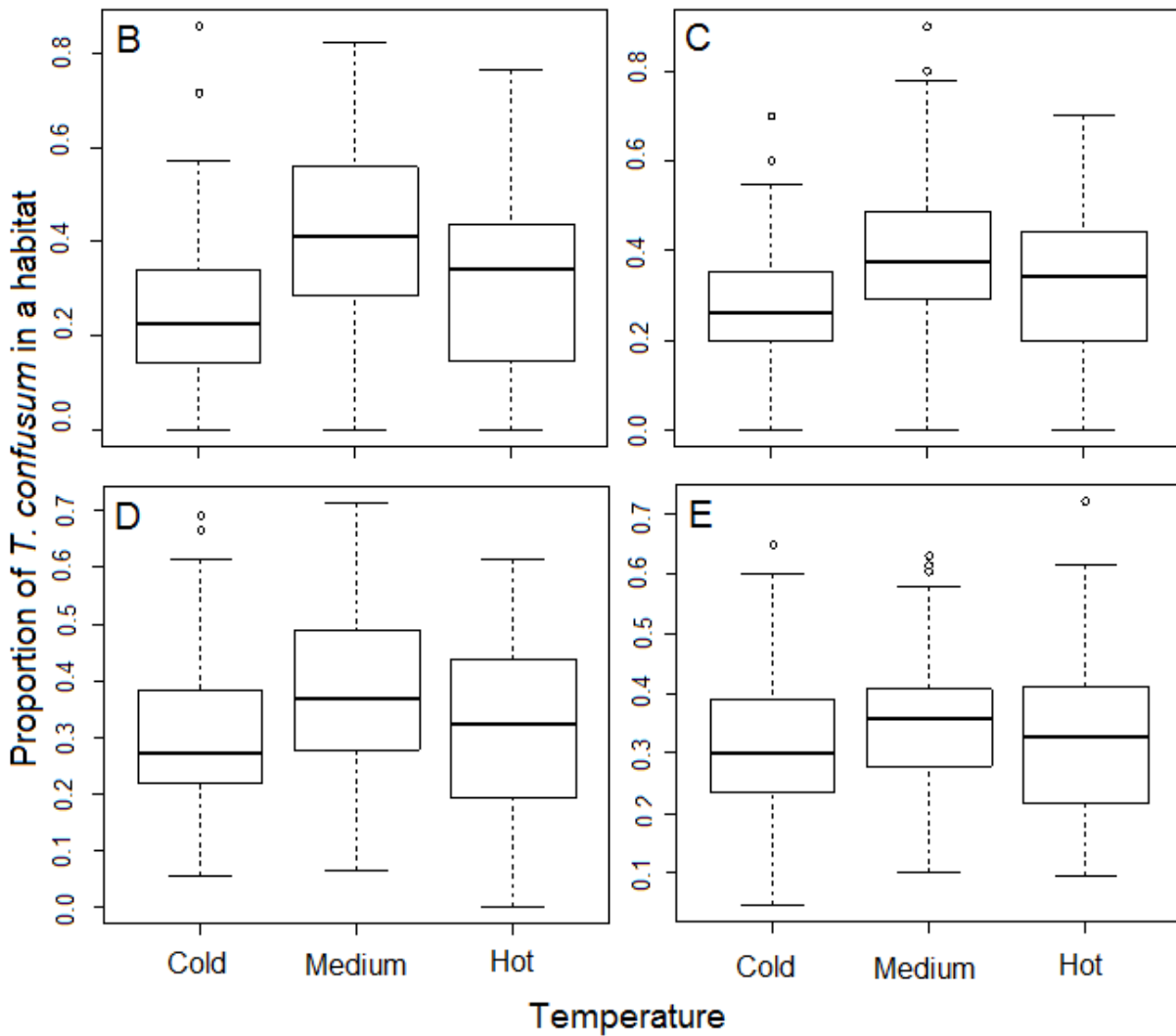
Figure 4. Proportion of *T. confusum* in a habitat at different species-ratio and temperatures. For the temperatures, cold=23°C, medium=28°C and hot=32°C. For the species ratio of *T. castaneum* to *T. confusum*, B=2:1, C=1:1, D=1:2 and E=0:1.

Figure 5. Proportion of *T. confusum* at different periods and temperatures. For the temperatures, cold=23°C, medium=28°C and hot=32°C. For the periods, X=weeks 1 to 4, Y=weeks 5 to 10 and Z=weeks 11 to 15.
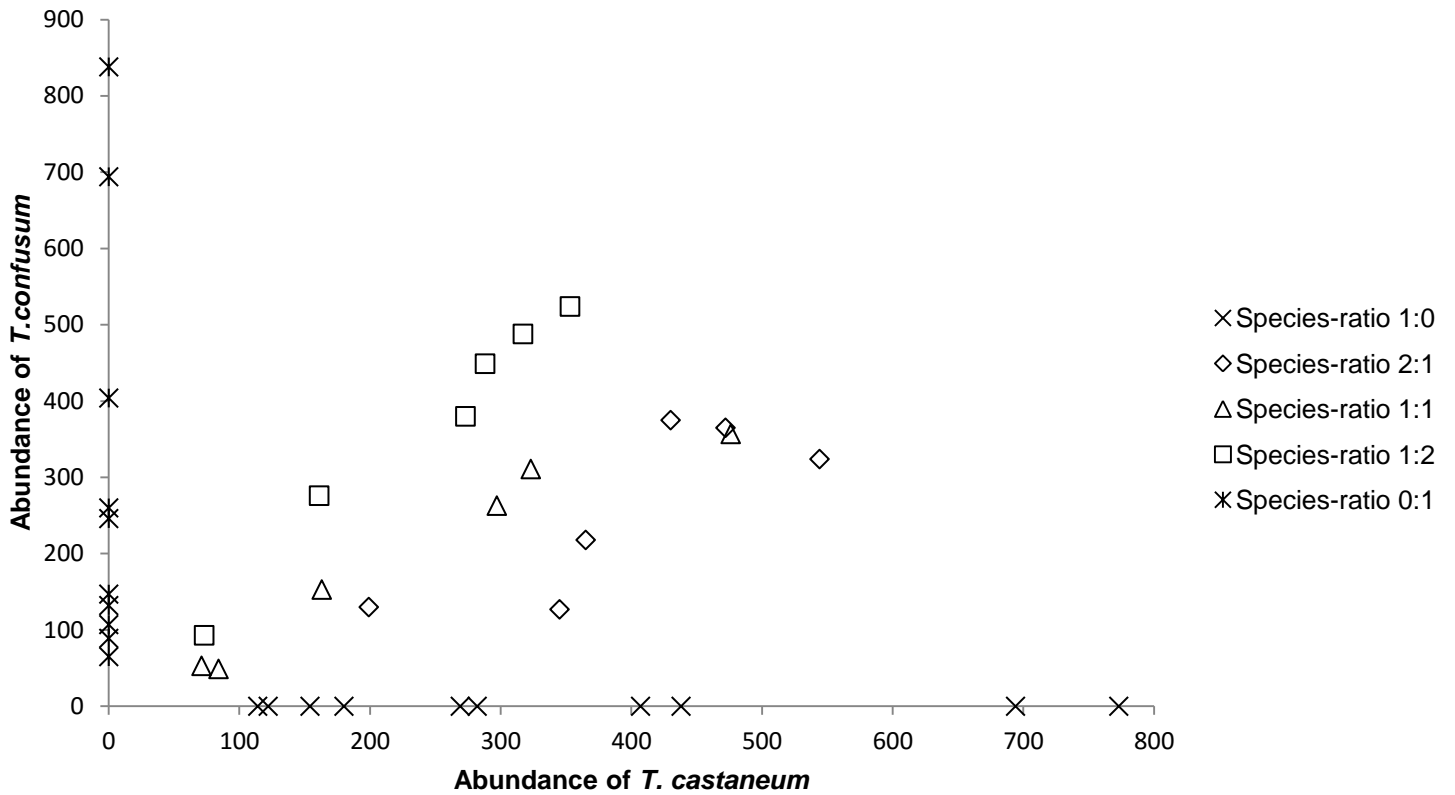
Figure 6. Abundance of *T. castaneum* compared to abundance of *T. confusum* in species ratio: 1:0, 2:1, 1:1, 1:2, and 0:1 based on the last week of data collection. Only the data collected on the 6 replicates for the last weeks have been analysed for treatments 2:1, 1:2 and 1:1. Each point represents one replicate. The final population size of each species differed between some treatments. However, the presence of *T. castaneum* did not affect the final population size of *T. confusum*, or vice versa, and the final population size did not differ between *T. castaneum* and *T. confusum*.