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# Competition between *Prostephanus truncatus* and *Sitophilus oryzae* on maize: the species that gets there first matters

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**Research Paper**

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## Abstract

Laboratory tests were carried out in order to examine the population growth of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrychidae) and *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) on maize. These two species were placed either simultaneously or one species was allowed to colonize the kernels 7 days earlier than the other, at two temperatures, 26 and 30 °C for 65 days. Apart from progeny production, grain quality parameters, such as insect-damaged kernels (IDK) and undamaged kernels (NDK), the weight of frass and kernel weight were measured. Our data confirms that temperature plays a key role in the competition of these two species; *P. truncatus* seems to perform better at the higher temperature (30 °C), regardless of the presence of an additional species. Moreover, the results of the present study demonstrates that *P. truncatus* outcompetes *S. oryzae*. *Sitophilus oryzae* produced fewer progeny than *P. truncatus* in all combinations. Given the outcome of a competition, we hypothesize that most of the kernel damage was due to feeding by *P. truncatus*. Based on these data, we surmise that *P. truncatus* has a competitive advantage as an invasive species in new areas with stored maize, even in the presence of *S. oryzae*.

## Introduction

Competition is one of the key elements that needs to be taken into account in invasion biology. Once introduced into a new geographical region, a potentially invasive species may be subjected to the presence of local competitors that are already established. The presence of these local competitors is often overlooked in many studies, especially where establishment models are primarily based in abiotic conditions, such as temperature and humidity (Arthur *et al.*, 2019), or only assess relationships of the invasive species with a few keystone predators or their absence in a new area. Nevertheless, it is well-established that certain alien and invasive species that occur in postharvest agricultural commodities are able to overcome competition and even displace other native species (Athanassiou *et al.*, 2014, 2017*b*; Kavallieratos *et al.*, 2017; Sakka and Athanassiou, 2018, Quellhorst *et al.*, 2020). For instance, Athanassiou *et al.* (2017*b*) found that the rice weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) could outcompete the maize weevil, *Sitophilus zeamais* Motschulsky and the granary weevil, *Sitophilus granarius* (L.) on rice (*Oryza* spp.) and maize (*Zea mays* L.). Additionally, Kavallieratos *et al.* (2017) found that an invasive species, the khapra beetle, *Trogoderma granarium* (Everts) (Coleoptera: Dermestidae), could outcompete and eventually displace other primary colonizers of stored grains, such as *S. oryzae* and the lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrychidae), when temperatures were 30 °C or higher.

One additional invasive species in stored product protection is the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrychidae). After its first introduction in western sub-Saharan Africa, which occurred approx. 40 years ago, this species has spread across several African countries, causing serious infestations on maize (Hodges *et al.*, 1983; Hodges, 1986; Addo *et al.*, 2002; Arthur *et al.*, 2019). Arthur *et al.* (2019) modeled the potential spread of this species in several parts of the world, and found that apart from North and South America, *P. truncatus* may find suitable areas in certain sub-tropical areas of Asia, where climate conditions are favorable. Nevertheless, even after its first introduction in Africa, *P. truncatus* was arrived to postharvest habitats already filled with other primary colonizers of stored maize, such as *S. zeamais*. Previous studies regarding the competition of these two species of maize indicated that *S. zeamais* was the dominant species at 25 °C, but at 30 °C the outcome was inconclusive (Giga and Canhao, 1993). More recently, Quellhorst *et al.* (2020) examined the competition of these two species on maize at four temperatures and found that increasing temperature resulted in elevated population growth of *P. truncatus* at the expense of *S. zeamais*. Moreover, the authors reported that when both species

were present, most of the damage on the maize kernels was due to the infestation by *P. truncatus* (Quellhorst *et al.*, 2020).

Although *S. zeamais* is commonly referred as the 'maize weevil', the relative *S. oryzae*, the 'rice weevil', is very often found infesting maize, probably in the same frequency at which *S. zeamais* is recorded on rice. In fact, the comparative origins of these two species are poorly understood, and considering the difficulties in their original identification, *S. zeamais* is often mistakenly referred to as *S. oryzae* if it is present on rice and vice versa. Nevertheless, Athanassiou and Buchelos (2001*a*) presented a survey of different storage facilities in Greece, and reported that both species coexisted in a considerable proportion of the samples taken. Athanassiou *et al.* (2017*b*) found that *S. oryzae* developed faster on rice and maize as compared with *S. zeamais*, but both species can coexist and co-infest the product. For example, in Portugal *S. zeamais* is the dominant species on stored rice when compared with *S. oryzae* (Carvalho *et al.*, 2013). Because *S. oryzae* has a strong presence in Africa, it is assumed that this species is a competitor of *P. truncatus* when an infestation occurs on maize. Moreover, *S. oryzae* may be more prevalent than *S. zeamais* at lower temperatures (Longstaff, 1981), so the competition of *S. oryzae* with *P. truncatus* is important to understand given where both species realistically co-occur, especially in overlaps of their range in colder areas (Arthur *et al.*, 2019).

The majority of the studies that examine competition in stored product beetles consider the simultaneous species' presence from the beginning of the infestation (Giga and Canhao, 1993; Mallqui *et al.*, 2013; Athanassiou *et al.*, 2014). Apparently, this is done to simplify the eventual competition model, based on the assumption that both species arrived together to the same food source. However, this scenario is rather unrealistic as usually a given species is either the first colonizer of the food source, or arrives in a food source that is already infested by another species. In a series of laboratory experiments with floor traps, Athanassiou *et al.* (2016) found that the response of the red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) was different, depending on the prior captures of the trap; thus, the existence of another species may alter the behavioral responses of the newly introduced one. This ecological succession characterizes stored product insects, as the primary colonizers begin an infestation on intact kernels, and then they are gradually substituted by the secondary colonizers, which are able to infest already damaged kernels (White, 1995; Trematerra *et al.*, 2000). Nevertheless, the subsequent colonization and competition of two primary colonizers at the same time on intact kernels have not been examined in detail. From competition theory, the first colonizer may have an advantage over the second one that will appear later, since it has more time to feed, lay eggs, and establish. On the other hand, the second colonizer may also have an advantage through development on already weakened commodities, which may accelerate feeding and reproduction. Thus, using *S. oryzae* and *P. truncatus* as model species, we examined their competition on maize, when these two species were placed either simultaneously or when one species colonized the kernel earlier than the other. To our knowledge, this is the first work that has examined the competition between these two species in this way to test founder effects.

## Materials and methods

### Insects

Adults (<7 days old) of *P. truncatus* and *S. oryzae* were obtained from insect colonies kept at the Laboratory of Entomology and Agricultural Zoology (LEAZ), Department of Agriculture, Crop Production and Rural Environment, University of Thessaly, Greece, on whole maize or whole wheat kernels, respectively, at 26 °C, 65% relative humidity (r.h.) and continuous darkness.

### Commodities

Clean and uninfested maize, *Zea mays* L. (var. Dias), was used in all experiments. Prior to the experiments, the maize was kept in −20 °C for over a week to eliminate any previous infestation, and then left for 3 days at ambient conditions. The moisture content of the kernels in the beginning of the experiments was approx. 14.2%, as determined by a moisture meter (Multitest, Gode SAS, Le Catelet, France).

### Competition experiment

Plastic cylindrical vials (3 cm in diameter, 8 cm high, Rotilabo Sample tins Snap on lid, Carl Roth, Germany) were the experimental units for these tests. Quantities of 20 g of maize were put separately inside the vials. The internal 'necks' of the vials were covered by Fluon (Northern Products Inc., Woonsocket, USA) to prevent the insects from moving away from the kernels. Then, the vials were divided into nine different competitive conditions (placements), in which the species were placed in the vials at different periods, as described above:

(i) Vials on which 6 adults of *P. truncatus* were placed on Day 0 (e.g. pure culture, immediate colonization),
(ii) Vials on which 6 adults of *S. oryzae* were placed on Day 0 (e.g. pure culture, immediate colonization),
(iii) Vials on which 6 adults of *P. truncatus* and 6 adults of *S. oryzae* were placed on Day 0 (e.g. mixed culture, simultaneous immediate colonization),
(iv) Vials on which 6 adults of *S. oryzae* were placed on Day 0, and 6 adults of *P. truncatus* were placed on Day 7 (7 days later) (e.g. mixed culture, *S. oryzae* founder),
(v) Vials on which 6 adults of *P. truncatus* were placed on Day 0, and 6 adults of *S. oryzae* were placed on Day 7 (e.g. mixed culture, *P. truncatus* founder),
(vi) Vials on which maize was placed on Day 0, and 6 adults of *S. oryzae* were placed on Day 7 (e.g. pure culture, delayed colonization),
(vii) Vials on which maize was placed on Day 0, and 6 adults of *P. truncatus* were placed on Day 7 (e.g. pure culture, delayed colonization),
(viii) Vials on which maize was placed on Day 0, and 6 adults of *S. oryzae* along with 6 adults of *P. truncatus* were placed on Day 7 (e.g. mixed culture, simultaneous delayed colonization) and
(ix) Vials on which only maize was placed on Day 0 (blank control).

After the introduction of the insects (Day 0), the vials were placed in incubators set at two temperatures, 26 and 32 °C and 65% r.h. in continuous darkness with separate sets of vials per temperature. For each temperature and competitive combination, there were 6 vials (e.g. replicates). On Day 65 (65 days after Day 0), the vials were opened and the number of dead and alive adults of each species were counted. Additionally, the number of insect-damaged kernels (IDK), weight of IDK, number of undamaged kernels (NDK), weight of NDK and the weight of frass were

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measured for each vial. To separate the progeny and frass from the kernels, a 2 × 2 mm sieve placed on top of a 1 × 1 mm sieve was used in combination with agitation. Afterwards, the frass, damaged, and undamaged kernels were weighed using a precision balance (Precisa 40SM-200A, Pag Oerlikon AG, Zurich, Switzerland). The blank control vials were not included in the analysis, as there were no insects and insect damage, but were kept during the entire experimental period and checked at the end visually for the presence of fungi.

### Data analysis

Levene's test was used to fulfill normality and homogeneity, and, when necessary, the data were log-transformed. Progeny production, IDK, NDK, the weight of IDK and NDK, and frass were analyzed by using a two-way ANOVA, separately for each species, with competitive condition and temperature as the main effects. Tukey–Kramer (HSD) test was used to compare means at $\alpha = 0.05$. When both species were present, additional post-hoc comparisons were made for progeny production within each combination between species, using a two-tailed *t*-test at n-2 *df*. The same paired comparison was carried out within each vial category for the quality characteristics, between the two temperatures.

## Results

### Progeny production

For both species, only insect competitive condition was significant (Table 1). At 26 °C, in vials that contained one species alone placed on Day 0, progeny production of *P. truncatus* was twice that of *S. oryzae* (fig. 1). Moreover, for the same vial category at 32 °C, both *P. truncatus* and *S. oryzae* produced a similar number of progeny as compared with 26 °C (fig. 2). Interestingly, for pure cultures of *S. oryzae* with delayed colonization, progeny production was lower than that of the vials that contained insects that had immediately colonized kernels on Day 0, for both temperatures tested. However, *P. truncatus* actually produced more progeny, at 26 and 32 °C, when colonization was delayed compared to when it was immediate on Day 0 (figs 1 and 2).

Considering the overall data, regardless of the specific competitive conditions in mixed cultures, progeny production of *S. oryzae* was lower than that of *P. truncatus*, with the latter species to have greater variations among combinations (figs 1 and 2). When the two species were placed together in the same vial on Day 0, at 26 °C, there were no significant differences between them in progeny production (Table 2). Moreover, *P. truncatus* progeny production was significantly increased in comparison with that of *S. oryzae*, when the two species were forced to delay colonization and simultaneously placed together on Day 7, but only at 26°C. Progeny production of *P. truncatus* was significantly higher even when parental adults of this species were delayed in colonization of the kernels 7 days later than *S. oryzae*, but only at 32 °C (Table 2). However, when *P. truncatus* was placed first, for both temperatures, progeny production was not significant higher than that of *S. oryzae*.

**Table 1.** ANOVA parameters for the adult progeny of each species in vials where parental adults had been placed at different intervals, at two temperatures (total *df* = 95)

| Insect species | | *P. truncatus* | | *S. oryzae* | |
|---|---|---|---|---|---|
| Source | *df* | *F* | *P* | *F* | *P* |
| Placement | 7 | 17.6 | <0.01 | 8.9 | <0.01 |
| Temperature | 1 | 3.7 | 0.05 | 0.4 | 0.51 |
| Placement × Temperature | 7 | 1.3 | 0.25 | 0.5 | 0.81 |

**Table 2:** T-test for progeny production within each combination between species (total *df* = 11)

| | 26°C | | 32°C | |
|---|---|---|---|---|
| Placement | t | *P* | t | *P* |
| Pt (0 d) | – | – | – | – |
| So (0 d) | – | – | – | – |
| So + Pt (0 d) | −0.4 | 0.67 | −1.2 | 0.27 |
| So (0 d) + Pt (7 d) | −1.4 | 0.19 | −4.5 | <0.01 |
| Pt (0 d) + So (7 d) | −1.9 | 0.09 | −2.0 | 0.09 |
| So (7 d) | – | – | – | – |
| Pt (7 d) | – | – | – | – |
| So + Pt (7 d) | −3.0 | 0.02 | −2.0 | 0.09 |

### Grain quality

No fungal detection was recorded in the blank controls, but there was some fungal development in some of the vials that contained maize with insects. Regarding frass, the main effects were significant, but their interaction was not (Table 3). Singificant differences of frass among the temperatures were found only in two of the cases tested here (Table 4). Regardless of significant differences, increasing temperature resulted in elevated frass production for both species (fig. 3). The lowest frass production was noted in the vials that contained only individuals of *S. oryzae* that had been placed on Day 0 or Day 7, for both temperatures. In general, more frass was recorded in vials that contained *P. truncatus*, either alone or with *S. oryzae*, as compared with the vials that contained *S. oryzae* alone.

For IDK number and weight, only insect placement was significant (Table 3). The lowest numbers of IDK were noted in vials containing *S. oryzae* that had been placed on Day 0 or Day 7. Moreover, in contrast with frass, the number of IDK were rather similar where both species were present, in most of the placements (fig. 4). Similarly, the weight of IDK was in accordance with the number of IDK in most of the vial categories, with the exception of the two categories in which *S. oryzae* was placed alone (fig. 5). Considering the data, the lowest weight of IDK was noted when *S. oryzae* was placed at Day 7, for both temperatures tested.

Both main effects and their interaction were significant for the number of NDK and the weight of NDK (Table 3). For the majority of the combinations tested, the number of NDK was similar for both temperatures (fig. 6). However, significant differences in the number of NDK were found between the two temperatures, where *S. oryzae* was placed 7 days after *P. truncatus* (0 d) in the vials and in the opposite of the latter case (Table 4). Similarly, NDK weight was significantly higher at 26 °C in two categories, when *P. truncatus* placed 7 days

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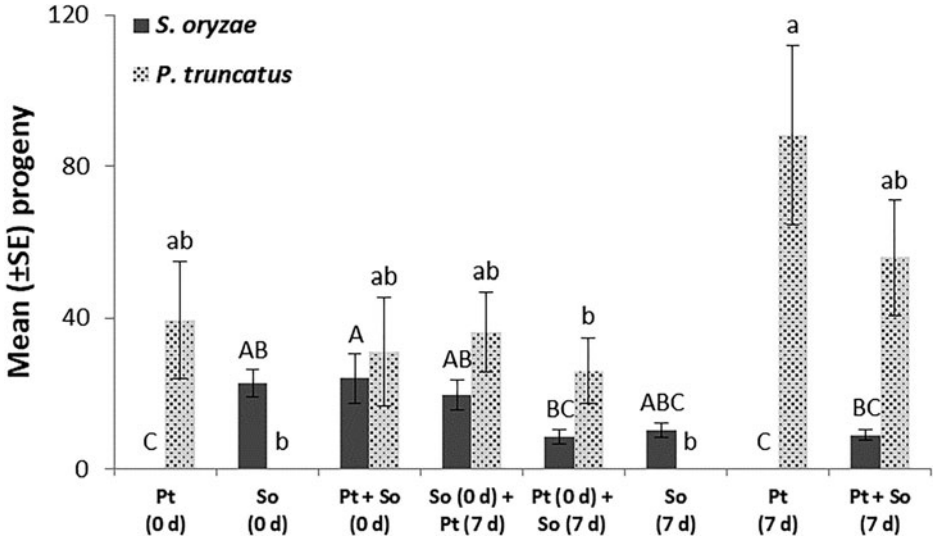


**Figure 1.** Mean (±SE) number of adults (dead and alive) of *S. oryzae* (black bars) or *P. truncatus* (gray bars) found per vial for every placement, when the vials were kept in 26 °C and 65% r.h. (Means followed by the same uppercase letter are not significantly different among placements for *S. oryzae*; means followed by the same lowercase letter are not significantly different among placements for *P. truncatus*; In all placements for *S. oryzae*, $F = 8.7$; $P < 0.01$; for *P. truncatus*, $F = 4.6$; $P < 0.01$. Total $df = 47$. HSD test at 0.05). So, *Sitophilus oryzae*; Pt, *Prostephanus truncatus*; d, day that species introduced into the vials.

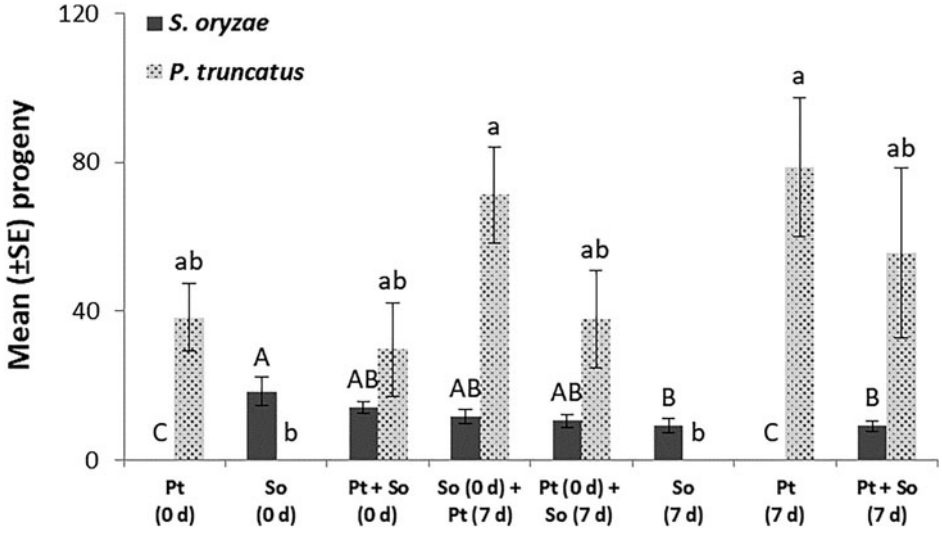


**Figure 2.** Mean (±SE) number of adults (dead and alive) of *S. oryzae* (black bars) or *P. truncatus* (gray bars) found per vial for every placement, when the vials were kept in 32 °C and 65% r.h. (Means followed by the same uppercase letter are not significantly different among placements for *S. oryzae*; means followed by the same lowercase letter are not significantly different among placements for *P. truncatus*; In all cases for *S. oryzae*, $F = 11.7$; $P < 0.01$. In all placements of *P. truncatus*, $F = 4.7$; $P < 0.01$. Total $df = 47$. HSD test at 0.05). So, *Sitophilus oryzae*; Pt, *Prostephanus truncatus*; d, day that species introduced into the vials.

**Table 3.** ANOVA parameters for frass, IDK weight, IDK number, NDK weight and NDK number in vials where parental adults had been placed at different intervals, at two temperatures (total $df = 95$)

| Insect species | | Frass | | IDK weight | | IDK number | | NDK weight | | NDK number | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Source | *df* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| Placement | 7 | 10.6 | <0.01 | 12.5 | <0.01 | 13.9 | <0.01 | 13.6 | <0.01 | 16.3 | <0.01 |
| Temp | 1 | 6.9 | <0.01 | 1.1 | 0.28 | 0.1 | 0.72 | 7.1 | <0.01 | 6.7 | 0.01 |
| Placement × Temp | 7 | 0.7 | 0.65 | 1.4 | 0.18 | 1.6 | 0.14 | 3.4 | <0.01 | 3.1 | <0.01 |

after the introduction of the *S. oryzae* in the same vials and in the opposite of the latter case (fig. 7). Adding the data for both temperatures, the highest weight of NDK was noted at 26 °C.

## Discussion

Our data confirm that temperature plays a key role in the competition of *P. truncatus* with *S. oryzae*, in the same way that has been already recorded for the competition of *P. truncatus* with *S. zeamais* (Giga and Canhao, 1993; Quellhorst *et al.*, 2020). Despite the fact that both beetle species are well-adapted to warm conditions (Longstaff, 1981; Bell and Watters, 1982), *P. truncatus* seems to perform better at temperatures that are 30 °C or higher, regardless of the presence of an additional species (Quellhorst *et al.*, 2020). Considering global warming, and the fact that *S. oryzae* is mostly adapted to temperate climates, while *S. zeamais* is adapted to sub-tropical climates, we hypothesize that in a possible invasion

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**Table 4:** T-test for quality characteristics within each placement between the two temperatures, 26 and 32°C (total *df* = 11)

| | Frass | | IDK weight | | IDK number | | NDK weight | | NDK number | |
|---|---|---|---|---|---|---|---|---|---|---|
| Placement | t | *P* | t | *P* | t | *P* | t | *P* | t | *P* |
| Pt (0 d) | 1.5 | 0.14 | 2.7 | 0.02 | 1.8 | 0.09 | −2.1 | 0.05 | −1.2 | 0.25 |
| So (0 d) | 1.7 | 0.12 | −0.9 | 0.38 | −1.0 | 0.30 | 0.7 | 0.44 | 0.7 | 0.47 |
| So + Pt (0 d) | 0.2 | 0.79 | −0.05 | 0.95 | −1.0 | 0.32 | 0.7 | 0.50 | 0.5 | 0.61 |
| So (0 d) + Pt (7 d) | 2.5 | 0.03 | 2.4 | 0.04 | 1.8 | 0.11 | −2.9 | 0.01 | −2.7 | 0.02 |
| Pt (0 d) + So (7 d) | 1.6 | 0.14 | 0.5 | 0.56 | 0.6 | 0.54 | −4.4 | <0.01 | −4.4 | <0.01 |
| So (7 d) | 2.6 | 0.03 | −1.7 | 0.12 | −2.5 | 0.03 | 1.4 | 0.19 | 0.5 | 0.59 |
| Pt (7 d) | 0.6 | 0.54 | 1.0 | 0.31 | 0.9 | 0.35 | −0.6 | 0.55 | −0.6 | 0.55 |
| So + Pt (7 d) | 0.4 | 0.67 | −0.6 | 0.50 | −1.2 | 0.25 | −0.1 | 0.89 | −0.07 | 0.94 |

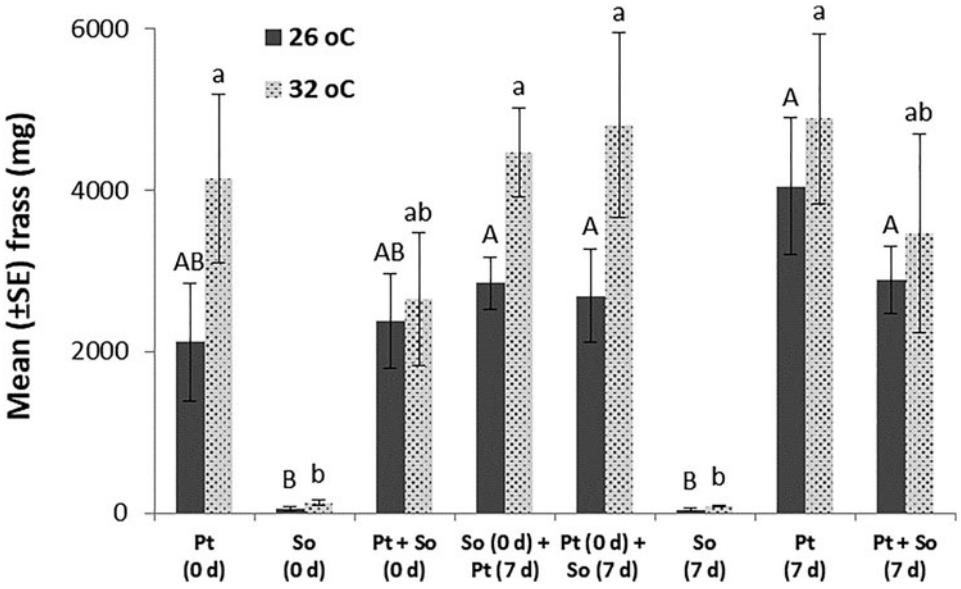


**Figure 3.** Mean (±SE) mg of frass found per vial for every placement, when the vials were kept in 26 or 32 °C and 65% r.h. (Means followed by the same uppercase letter are not significantly different between insect placements at 26 °C; means followed by the same lowercase letter are not significantly different between insect placements at 32 °C; In all placements at 26 °C: $F = 7.1$; $P < 0.01$; at 32 °C: $F = 5.1$; $P < 0.01$ Total $df = 47$. HSD test at 0.05). °C, Temperature in Celsius; So, *Sitophilus oryzae*; Pt, *Prostephanus truncatus*; d, day that species introduced into the vials.

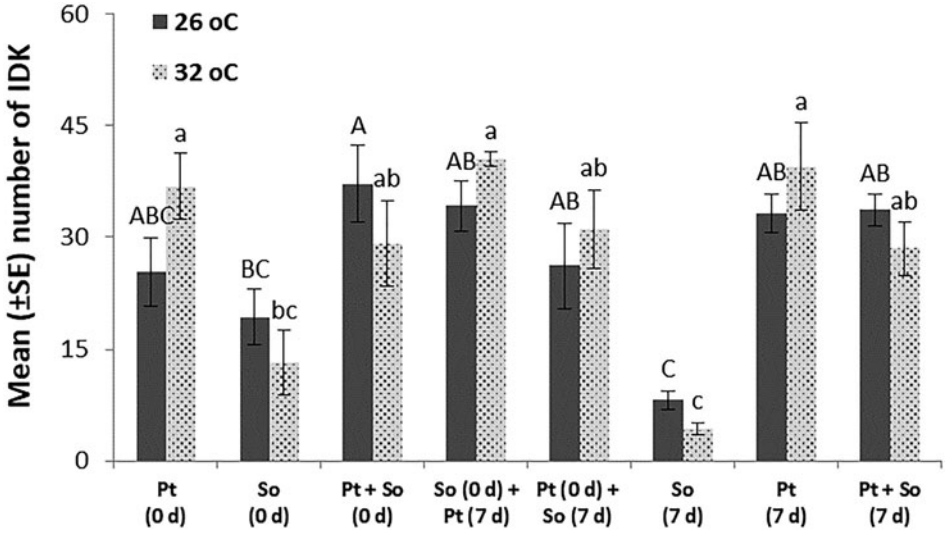


**Figure 4.** Mean (±SE) number of kernels that had one or more holes from the insects (IDK) found per vial for every placement, when the vials were kept in 26 or 32 °C and 65% r.h. (Means followed by the same uppercase letter are not significantly different; means followed by the same lowercase letter are not significantly different; in all placements at 26 °C: $F = 6.3$; $P < 0.01$; at 32 °C: $F = 8.9$; $P < 0.01$.Total $df = 47$. HSD test at 0.05). °C, Temperature in Celsius; So, *Sitophilus oryzae*; Pt, *Prostephanus truncatus*; d, day that species introduced into the vials.

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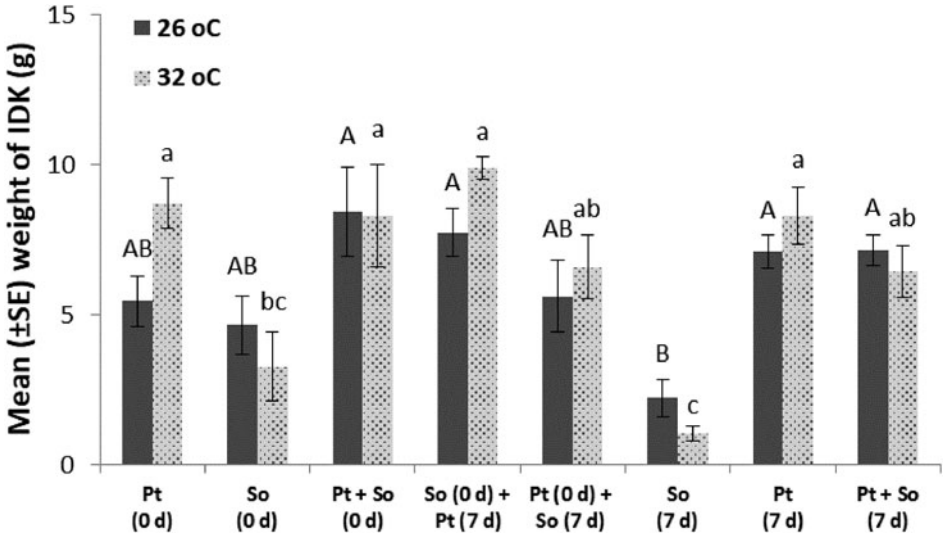


**Figure 5.** Mean (±SE) weight (g) of kernels that had one or more holes from the insects (IDK) and found per vial for every placement, when the vials were kept in 26 or 32 °C and 65% r.h. (Means followed by the same uppercase letter are not significantly different; means followed by the same lowercase letter are not significantly different; in all cases 26 °C, $F = 4.6$; $P < 0.01$. In all placements of 32 °C, $F = 9.1$; $P < 0.01$.Total $df = 47$. HSD test at 0.05). IDK, Insect Damaged Kernels; °C, Temperature in Celsius; So, *Sitophilus oryzae*; Pt, *Prostephanus truncatus*; d, day that species introduced into the vials.

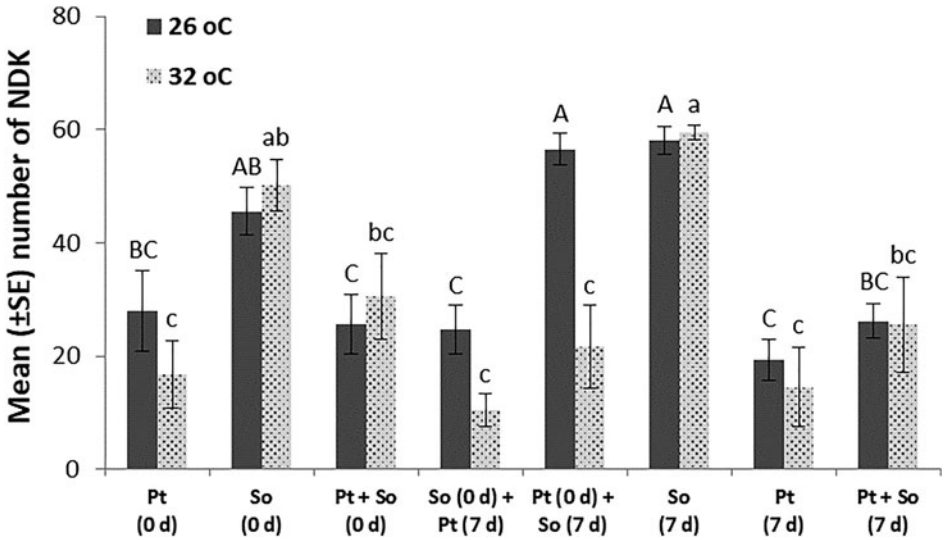


**Figure 6.** Mean (±SE) number of whole kernels without any damage from insects (NDK) found per vial for every placement, when the vials were kept in 26 or 32 °C and 65% r.h. (Means followed by the same uppercase letter are not significantly different; means followed by the same lowercase letter are not significantly different; in all placements at 26 °C, $F = 12.5$; $P < 0.01$. In all placements of 32 °C, $F = 8.3$; $P < 0.01$.Total $df = 47$. HSD test at 0.05). NDK, Undamaged Kernels; °C, Temperature in Celsius; So, *Sitophilus oryzae*; Pt, *Prostephanus truncatus*; d, day that species introduced into the vials.

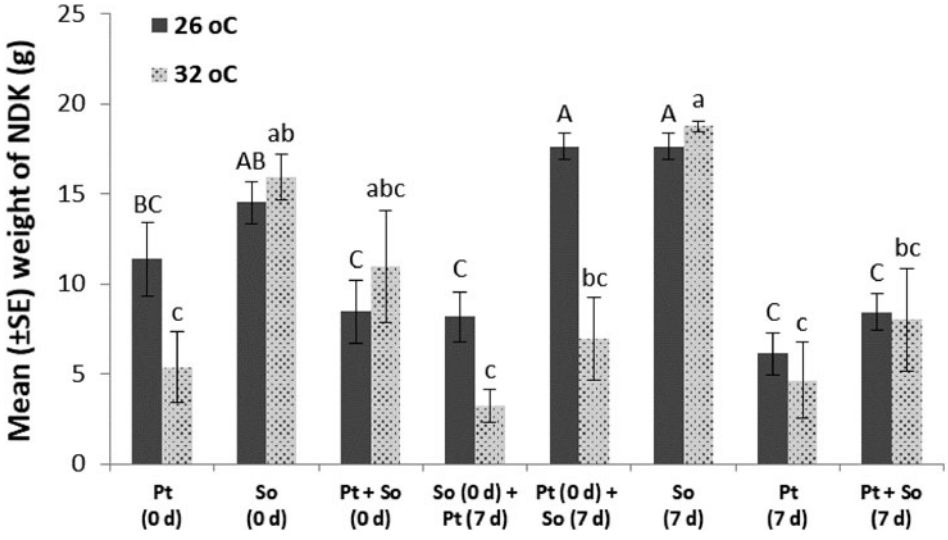


**Figure 7.** Mean (±SE) weight (g) of whole kernels without any damage from insects (NDK), found per vial for every placement, when the vials were kept in 26 or 32 °C and 65% r.h. (Means followed by the same uppercase letter are not significantly different; means followed by the same lowercase letter are not significantly different; in all cases at 26 °C, $F = 11.7$; $P < 0.01$. In all placements of 32 °C, $F = 7.2$; $P < 0.01$. Total $df = 47$. HSD test at 0.05). NDK, Undamaged Kernels; °C, Temperature in Celsius; So, *Sitophilus oryzae*; Pt, *Prostephanus truncatus*; d, day that species introduced into the vials.

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of stored maize in new areas, *P. truncatus* may have an advantage over both species of weevils. Moreover, under this scenario, displacement may occur due to the fact that *Sitophilus* spp. have a wide range of grains that can infest as hosts, while *P. truncatus* is mostly limited to maize and cassava (Hagstrum and Subramanyam, 2009; Athanassiou *et al.*, 2017*a*).

For the competition of *P. truncatus* with *S. zeamais*, Quellhorst *et al.* (2020) examined temperatures ranging between 20 and 35 °C and found that *S. zeamais* population growth was better than that of *P. truncatus* at 25 °C, but there was a considerable growth cost when both species were together. At 35 °C however, the population of *S. zeamais* collapses, as this is considered a temperature that is close to the upper thermal requirements for this species (Throne, 1994). In a similar way, we have found that 32 °C can be considered as close to the upper thermal threshold for *S. oryzae*, as the number of progeny produced was much lower than that of 26 °C. In some of the vials tested, we observed considerable mold development due to insect feeding, which might have influenced insect development and population growth. Although we did not record quantitative data regarding mold development, we observed that the presence of mold caused more detrimental effects on *S. oryzae* growth than on *P. truncatus* growth. In their competition experiment, Quellhorst *et al.* (2020) also reported fungal development, which was identified as *Aspergillus flavus* (Eurotiales: Trichocomaceae). Moreover, mold was mostly associated with the presence of *S. zeamais* in the vials and not with *P. truncatus* (Quellhorst *et al.*, 2020), clearly indicating that *S. zeamais* contributes to fungal development, and perhaps eventually damaged by the presence of fungi. Our observations suggest than this may be also true in the case of *S. oryzae*.

The placement of the parental individuals at different colonization intervals had both positive and negative effects on their population growth. Paradoxically, for *S. oryzae*, progeny production was lower when parental adults were delayed in colonizing kernels (e.g. Day 7) as compared with Day 0. This could be related again with fungal presence, as the critical time for mold development was shorter when insects were placed 7 days later, causing less detrimental effects in progeny production capacity. However, higher progeny production at shorter developmental periods was recorded in the case of *P. truncatus*. When both species were placed on Day 7, *P. truncatus* had a higher progeny production than *S. oryzae*. This difference can be considered an outcome of the reduced presence of *S. oryzae* (i.e. reduced competition), rather than a faster developmental rate of *P. truncatus* on maize at shorter intervals. Giga and Canhao (1993) reported that *P. truncatus* is well-adapted at 30 °C when competing with *S. zeamais*, having its optimum development at 32 °C (Bell and Watters, 1982; Howard, 1983; Hodges, 1986). In our study, we saw that at this optimum temperature (32 °C) *P. truncatus* dominated over *S. oryzae*, regardless of the presence of the latter species. On the other hand, at 26 °C, *P. truncatus* also performed better than *S. oryzae* when both were present, regardless of the time of placement of the parental adults. Based on this, we postulate that *P. truncatus* population growth was better adapted than that of *S. oryzae* to the different times of insect placement, indicating that this species is the superior competitor in our study. Howard (1983) reported that *P. truncatus* can gradually predominate over *S. zeamais* even in maize with temperatures that are higher than 28 °C; our data show that this is probably true in the case of *S. oryzae* as well.

All the above are indicative of the potential of *P. truncatus* for rapid development and spread, even if it develops in maize already colonized by another species. In fact, the presence of frass is beneficial for the larval development of this species, especially at their early instars (Hodges, 1986, 2002). Still, Athanassiou *et al.* (2016) found that all immatures of *P. truncatus* were inside the kernels and not in the dust outside of the kernels. Hence, this species can easily develop without frass, but the frass may serve as a deterrent or inhibitor to other competitors and may be able to positively utilize frass for its own development. Thus, the frass production in already infested kernels by *Sitophilus* spp. may also enhance *P. truncatus* population growth. Moreover, the results of the present study demonstrate that when *P. truncatus* was the first species that was introduced in the vials, it outcompeted *S. oryzae*, but the reverse was not true. When *P. truncatus* was introduced second, it still displaced *S. oryzae*, when temperatures were favorable. None of the mixed cultures tested here resulted in higher progeny production by *S. oryzae* than *P. truncatus*, with the exception of vials that contained only pure cultures of *S. oryzae*.

Considering the comparable data among the different competitive conditions, we hypothesize that most of the kernel damage was due to the infestation of *P. truncatus*. Similar results have been reported in the competition of *P. truncatus* with *S. zeamais* (Quellhorst *et al.*, 2020). The reduced frass production when *S. oryzae* was the only species in the vial, especially when the parental adults had been placed on Day 0, can be regarded as an indicator that this species does not consume/damage the both temperatures, with only a slight increase at 32 °C, indicating that kernel damage may not be directly proportional with the number of insects inside the vials, where food availability is a limiting factor. Interestingly, the IDK and the NDK were not always directly proportional, probably due to variations of the number of kernels used from vial to vial, but also because *P. truncatus* can create more holes on the kernels than *S. oryzae*.

In summary, the results of the present work show that there are rather limited competitive costs of *P. truncatus* colonizing environments with *S. oryzae* already present. Conversely, there were noticeable reductions in progeny production of *S. oryzae* when this species was present with *P. truncatus*, but this may not constitute an actual competitive cost, and may be mostly related with mold development. Colonization of kernels by *P. truncatus* before other species may give an additional competitive advantage, but it already has so many advantages over other species, that one more may not be overly important, since it can already outcompete *S. oryzae* that has already infested kernels. Based on these data, we hypothesize that *P. truncatus* has a competitive advantage as an invasive species in new areas with stored maize, even in the presence of *S. oryzae* (and possibly other colonizers), and can easily develop at 26 °C, which is a typical temperature of grain bulks in temperate climates during a large part of the storage period (Athanassiou and Buchelos, 2001*b*, 2020). All the above indicates that *P. truncatus* has high potential for further spread, and this should be seriously taken into account in predicative modeling and regulatory approaches.

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## References


**Addo S, Birkinsaw LA and Hodges RJ** (2002) Ten years after the arrival in Ghana of larger grain borer: farmer's responses and adoption of IPM strategies. *International Journal of Pest Management* **48**, 315–325.

**Arthur FH, Morrison WR and Morey AC** (2019) Modeling the potential range expansion of larger grain borer, *Prostephanus truncatus* (Coleoptera: Bostrichidae). *Scientific Reports* **9**, 6862.

**Athanassiou CG and Buchelos CT** (2001*a*) The presence of *Sitophilus zeamais* Motschulsky 1855 (Coleoptera: Curculionidae) in Greece: distribution and food preferences. *Annual Benaki Phytopathology Institute* **19**, 140–144.

**Athanassiou CG and Buchelos CT** (2001*b*) Detection of stored-wheat beetle species and estimation of population density using unbaited probe traps and grain trier samples. *Entomologia Experimentalis et Applicata* **98**, 67–78.

**Athanassiou CG and Buchelos CT** (2020) Grain properties and insect distribution trends in silos of wheat. *Journal of Stored Products Research* **88**, 101632.

**Athanassiou CG, Kavallieratos NG, Throne JE and Nakas CT** (2014) Competition among species of stored-product psocids (Psocoptera) in stored grain. *PLoS One* **9**, 102867.

**Athanassiou CG, Kavallieratos NG and Campbell JF** (2016) Capture of *Tribolium castaneum* and *Tribolium confusum* (Coleoptera: Tenebrionidae) in floor traps: the effect of previous captures. *Journal of Economic Entomology* **109**, 461–466.

**Athanassiou CG, Kavallieratos NG, Boukouvala MC and Nika EP** (2017*a*) Influence of commodity on the population growth of the larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrychidae). *Journal of Stored Products Research* **73**, 129–134.

**Athanassiou CG, Kavallieratos NG and Campbell JF** (2017*b*) Competition of three species of *Sitophilus* on rice and maize. *PLoS One* **12**, 0173377.

**Bell RJ and Watters FL** (1982) Environmental factors influencing the development and rate of increase of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) on stored maize. *Journal of Stored Product Research* **18**, 131–142.

**Carvalho MO, Faro A and Subramanyam B** (2013) Insect population distribution and density estimates in a large rice mill in Portugal – a pilot study. *Journal of Stored Products Research* **52**, 48–56.

**Giga DP and Canhao SRJ** (1993) Competition between *Prostephanus truncatus* (Horn) and *Sitophilus zeamais* (Motsch.) in maize at two temperatures. *Journal of Stored Product Research* **29**, 63–70.

**Hagstrum DW and Subramanyam B** (2009) *Stored–Product Insect Resource*. St. Paul, MN: AACC International Inc.

**Hodges RJ** (1986) The biology and control of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) – a destructive storage pest with an increasing range. *Journal of Stored Product Research* **22**, 1–14.

**Hodges RJ** (2002) Detection and monitoring of larger grain borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). *Integrated Pest Management Reviews* **7**, 223–243.

**Hodges RJ, Dunstan WR, Magazini I and Golob P** (1983) An outbreak of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) in East Africa (Tabora, Tanzania). *Protection Ecology* **5**, 183–194.

**Howard DC** (1983) *The Population Biology of the Greater Grain Borer, Prostephanus truncatus (Horn)* (Doctoral dissertation), University of Reading, UK.

**Kavallieratos NG, Athanassiou CG, Guedes RNC, Drempela JD and Boukouvala MC** (2017) Invader competition with local competitors: displacement or coexistence among the invasive khapra beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae), and two other major stored - grain beetles? *Frontiers in Plant Science* **8**, 1837.

**Longstaff BC** (1981) Biology of the grain pests of the genus *Sitophilus* (Coleoptera: Curculionidae): a critical review. *Protection Ecology* **2**, 83–130.

**Mallqui KSV, Oliveira EE and Guedes RNC** (2013) Competition between the bean weevils *Acanthoscelides obtectus* and *Zabrotes subfasciatus* in common beans. *Journal of Stored Products Research* **55**, 32–35.

**Quellhorst H, Athanassiou CG, Bruce A, Scully ED and Morrison WR** (2020) Temperature-mediated competition between the invasive larger grain borer (Coleoptera: Bostrichidae) and the cosmopolitan maize weevil (Coleoptera: Curculionidae). *Environmental Entomology* **49**, 255–264.

**Sakka MK and Athanassiou CG** (2018) Competition of three stored-product bostrychids on different temperatures and commodities. *Journal of Stored Product Research* **79**, 34–39.

**Throne JE** (1994) Life history of immature maize weevils (Coleoptera: Curculionidae) on corn stored at constant temperatures and relative humidities in the laboratory. *Environmental Entomology* **23**, 1459–1471.

**Trematerra P, Sciarreta A and Tamasi E** (2000) Behavioral responses of *Oryzaephilus surinamensis, Tribolium castaneum* and *Tribolium confusum* to naturally and artificially damaged durum wheat kernels. *Entomologia Experimentalis et Applicata* **94**, 195–200.

**White NDG** (1995) Insects, mites and insecticides in stored-grain ecosystems. In Jayas DS, White NDG and Muir WE (eds), *Stored-grain Ecosystems*. New York: Marcel Dekker Inc., pp. 123–167.


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