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Interspecific associations among stored-grain beetles

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ABSTRACT

Recent increases in prices of raw grain, including wheat, will reduce action thresholds for insect damage and therefore justify more research into management practices and understanding of pest ecology in stored grain. Compared to most other habitats, natural or man-made, a filled grain silo constitutes a unique and fairly homogeneous habitat in which food availability for many grain-feeding insects is unlimited. A fundamental aspect of stored-grain insect ecology is a better understanding of associations among common beetle species. We analyzed the densities of three important stored-grain beetle species, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Laemophloeidae), and *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) in wheat samples collected in 1999–2001 from 129 grain silos in Kansas. The beetles studied here are highly mobile, and the number of insects in each grain sample is a result of the beetles' preference for favorable micro-environmental conditions and possibly of intra- and interspecific associations. In general, the number of *T. castaneum* in a grain sample increased as the number of *R. dominica* increased, but the number of *C. ferrugineus* was not correlated with the number of *R. dominica*. The densities of both *T. castaneum* and *R. dominica* decreased as the number of *C. ferrugineus* increased. *Cryptolestes ferrugineus* and *T. castaneum* can be predators and the species composition of insects in a grain sample may be modified by predation. As *T. castaneum* populations increased, so did *R. dominica* but not *C. ferrugineus*. Our analysis of the species composition in grain samples is discussed in an ecological context.

1. Introduction

Compared to most other habitats, natural or man-made, a silo full of grain constitutes a uniquely uniform habitat. North American grain storage structures typically hold hundreds or thousands of metric tons of grain (Sinha et al., 1969b; Nansen et al., 2004a; Flinn et al., 2004b; Toews et al., 2005). Because of the physical structure of grain silos, resource exchange with the surrounding environment is almost negligible (excluding migration/immigration of rodents and insects associated with the grain mass), and grain silos are well protected against diurnal fluctuations. There are no physical barriers inside grain silos and beetles readily use inter-kernel spaces for movement; therefore, search time for a new food kernel is negligible. Foreign material in stored grain represents about 1–5% (w/w) (Fang et al., 2002; Flinn et al., 2004a; Toews et al., 2005), so grain and associated cereal micro-organisms are the only food sources present. Grain is often stored for six months or longer, during which time insects can complete several generations. Within the storage period, there is considerably less phenological change in the grain than is typically seen in growing plants or other insect hosts, so stored grain can be considered a relatively stable host. Also, life history studies of different stored-grain insects (Hagstrum and Milliken, 1988; Jacob and Fleming, 1989; Subramanyam and Hagstrum, 1993; Throne, 1994; Beckett et al., 1999) have shown that, while species certainly have optimum conditions, they can complete their life cycle over the range of abiotic conditions commonly found in grain silos.

Given virtually unlimited food availability in a fairly stable environment, such as a grain silo, what is the role of interspecific associations among stored-grain pests? While there are many studies on interspecific associations among stored-grain insects under controlled and highly constrained laboratory conditions (e.g. mason jars), only few studies are based on data from naturally infested storage systems. Previous studies on stored-grain insects (Hagstrum et al., 1985; Nansen et al., 2004a) have shown a markedly uneven distribution of insect density among grain samples,

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and this variation was only loosely associated with abiotic conditions. After several months of storage, which typically coincides with decrease in ambient temperatures, the biophysical conditions in stored grain tend to become less homogeneous and temperature and grain moisture gradients develop (White and Sinha, 1980; Barak and Harein, 1981; Hagstrum et al., 1985; Hagstrum, 1987; Arthur and Flinn, 2000; Nansen et al., 2004b). Thus, spatio-temporal variations in abiotic conditions within a grain mass and among samples may partly explain the uneven distribution of insect pests (McGregor, 1964; Hagstrum et al., 1998; Jian and Jayas, 2009). *Cryptolestes ferrugineus* (Stephens) (Coleoptera: Laemophloeidae) and *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) can be predators (Hagstrum and Gilbert, 1976; Suresh et al., 2001) and the numbers of insects in grain samples may have been modified by predation and/or other interspecific associations.

In this study, we compared counts of adult *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), *C. ferrugineus*, and *T. castaneum* in a large number of wheat samples collected in 1999–2001 from commercial grain silos in Kansas. These three beetle species are among the most common pests found in wheat stored in Kansas (Reed et al., 1991 and many other studies). In terms of potential damage to stored grain, *R. dominica* is more economically important than the other two beetle species because *R. dominica* develops inside the kernels, which leads to insect fragments in flour when infested wheat is milled. *Cryptolestes ferrugineus* is considered a secondary granivore. Even though larvae of *C. ferrugineus* may feed within the germ of the kernel, infestations do not result in insect fragments in flour because the germ is separated from the endosperm during milling. Their presence (if alive) may trigger price discounts at the point of sale due to the special category "infested" applied during grading when two or more live insects injurious to wheat are found in grading samples (Anonymous, 1994). *Tribolium castaneum* is also considered a secondary pest, because it does not feed on undamaged kernels (White, 1982; Lhaloui et al., 1988). The main objective of this project was to characterize the associations between beetle sample counts, discuss them in an ecological context, highlight needs for additional research, and provide suggestions concerning how such interspecific associations may be incorporated into ecological models of stored-grain population dynamics.

2. Materials and methods

2.1. Grain elevators and grain sampling

An areawide integrated pest management program for grain elevators was started in 1998 (Flinn et al., 2003, 2007; Hagstrum et al., 2008). Silos at these grain elevators were upright concrete bins, typically 6–9 m in diameter and 30–35 m tall. Maize and other grains were stored in separate bins in the project elevators, but only wheat was sampled during this project. Wheat grain samples were collected with a vacuum-probe, Port-A-Probe (Grain Value Systems, Shawnee Mission Kansas), which consists of a vacuum pump powered by a 5.3-kW gasoline engine connected by flexible plastic tubing to sections of rigid aluminium tubes 1.2 m long by 3.5 cm wide. Probes were inserted vertically into the grain and a 3.9 l (about 3 kg) sample of wheat was taken during every 1.2 m transect of grain to a depth of 12 m. The grain was sampled through the entry port at the top of the bin. Grain samples were extracted from the grain mass by suction and collected in a cyclone funnel. To extract insects from grain samples, each sample was processed twice over an inclined sieve (89 by 43 cm, 1.6 mm aperture) (Hagstrum, 1989) to separate insects from the wheat. Material that passed through the screen was collected on a pan below the screen, and then slid into a funnel at the bottom of the pan. A re-sealable plastic bag was attached to the funnel to collect this material. A hopper above the screen held the grain sample and a funnel at the base of the screen directed material passing over the screen into a plastic bucket. The sieve was inclined 24° from horizontal and the opening of the hopper was adjusted such that the sample passed over the screen in about 25 s. In a typical bin (6–9 m wide and 30–35 m tall), the sampling rate for vacuum-probe samples was 0.07–0.13 kg per t of grain sampled. Four species of natural enemies were found in the grain samples: *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae), *Anisopteromalus calandrae* (Howard) (Hymenoptera: Pteromalidae), *Theocolax elegans* (Westwood) (Hymenoptera: Pteromalidae), and *Cephalonomia waterstoni* Gahan (Hymenoptera: Bethylidae), but they were not considered further in this study. Likewise, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) (313 individuals in total) and *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae) (159 individuals) had low average densities ($<$0.40 beetles per kg in all three years), and occurred in $<$6% of samples, so these two species were not considered further.

2.2. Data analysis

We used the response surface regression procedure (PROC RSREG) in SAS/STAT 8.00 for Windows (SAS Institute, Cary NC), which examines linear and quadratic effects and linear interactions of independent variables. Further details on the use of the response surface regression procedure are available in Freund and Littell (1991). This regression approach was used to investigate interspecific associations among the three beetle species in which insect counts per grain sample of one species were used as the dependent variable with counts of the other two species as explanatory variables. The three beetle species investigated in this study are known to have considerable variation in their vertical distribution within grain silos (Hagstrum, 1989; Flinn et al., 2004a; Nansen et al., 2004b), so separate regression analysis was conducted for "top samples" (collected from 0 to 120 cm below the grain surface) and "lower samples" (120–240 cm below the grain surface). Maximum beetle counts in a single grain sample were: 3009 *C. ferrugineus*, 2320 *R. dominica*, and 578 *T. castaneum*, but such extreme counts were expected to have disproportionally high impact on the analyses and were therefore discarded. Consequently, counts from a grain sample were only included if the total sum of the three species was $>$0 (at least one beetle was present) and if the count of one of the three species did not exceed 100 individuals. Thus, only counts from samples with low to medium beetle densities were included in regression analyses.

3. Results

3.1. Grain storage facilities and insects identified

In the original data set, grain samples were collected from 11 grain elevators, each with 2–53 grain silos. Among the 129 sampled grain silos, 30 were sampled once, and the maximum number of samples obtained from a single silo was 42 (average = 5.7). A total of 7225 grain samples were collected, but only 1065 (15%) contained at least one beetle of the three species examined and at the same time did not have more than 100 individuals of any of the three species. Of these 1065 samples, 194 were "top samples" and 871 were "lower samples". *Rhyzopertha dominica* was the most abundant insect found (26,255 individuals), followed by *C. ferrugineus* (12,042 individuals), *T. castaneum* (7812 individuals). We observed considerable variation in beetle densities both vertically within a grain silo and among adjacent silos. Highest total beetle density in a single sample exceeded 5900 beetles and was collected in November 2000 from the top 1.2 m. In the same silo, all grain samples collected up to 9 m below the surface contained insects, but the beetle density decreased exponentially. No beetles were found in several of the adjacent silos, which were sampled on the same date. In another grain silo, as many as 1800 beetles per sample were found in the first 1.2 m sample, while no beetles were found in a sample collected 1.2–2.4 m below the grain surface.

We examined 1065 grain samples containing at least one adult of the three species and not more than 100 individuals of any of the three species and found that *R. dominica* occurred by itself in about 11% of the samples, *C. ferrugineus* in 38%, and *T. castaneum* in 13% (Table 1). For all three species, very few grain samples contained more than 20 individuals of each species (Fig. 1). In general, beetle densities were higher in top samples compared to lower samples. In samples with only *C. ferrugineus* or only *T. castaneum*, the average beetle density was 2–5 times less than in grain samples which only contained *R. dominica*. However, a fairly high number of grain samples contained only *C. ferrugineus* or only *T. castaneum*, while comparatively less grain samples only contained *R. dominica*. When only *C. ferrugineus* and *T. castaneum* were present, the beetle density was also lower than when *R. dominica* was present. Meanwhile, the beetle density was similar in grain samples only containing *R. dominica* or *R. dominica* and one of the other two species. The highest average beetle density was found in grain samples that contained all three species.

3.2. Regression analyses

Table 2 summarizes the regression results of the pairwise analyses of how counts of one beetle species appeared to be affected by those of the two other species. For top and lower samples, counts of *R. dominica* and *T. castaneum* were significantly correlated with counts of C. *ferrugineus* ($P < 0.05$) but only explained 13% (top samples) and 4% (lower samples) of the total variance, so these associations were not analyzed further. Regarding regression analyses of *R. dominica* and *T. castaneum*, we found that for both species, the highest R^2-values were obtained in analysis of top samples in which over 30% of the variability was explained, compared to lower samples. While negative population densities clearly do not exist, they can be interpreted as one species having a strong adverse effect on the population density of another species.

We used the linear and quadratic coefficients in Table 2 to generate regression surfaces of explanatory beetle densities from 1 to 100, and in top samples it was seen that counts of *R. dominica* (Fig. 2a): 1) decreased as counts of C. *ferrugineus* increased, especially when those of *T. castaneum* were low, 2) were positively associated with increasing numbers of *T. castaneum*, and 3) *R. dominica* density was predicted to be lowest (negative, meaning very low) when *T. castaneum* was absent and C. *ferrugineus* density was >60 per grain sample (20 per kg). Regarding regression analysis of *T. castaneum* counts (Fig. 2b): 1) they were positively associated with those of *R. dominica* but did not show a clear/consistent response to those of *C. ferrugineus*. Highest *T. castaneum*

Table 1
Mean beetle densities in top and lower grain samples with different combinations of beetle species.

Beetles in samples	Lower samples		Top samples	
	Samples	Density	Samples	Density
R. dominica only	107	11.1	11	17.4
C. ferrugineus only	341	2.9	65	6.4
T. castaneum only	114	2.6	28	8.2
C. ferrugineus and *R. dominica* only	58	14.4	13	14.7
R. dominica and *T. castaneum* only	35	23.1	4	33.3
C. ferrugineus and *T. castaneum* only	123	10.1	38	19.4
C. ferrugineus and *R. dominica* and *T. castaneum*	93	44.55	35	57.9

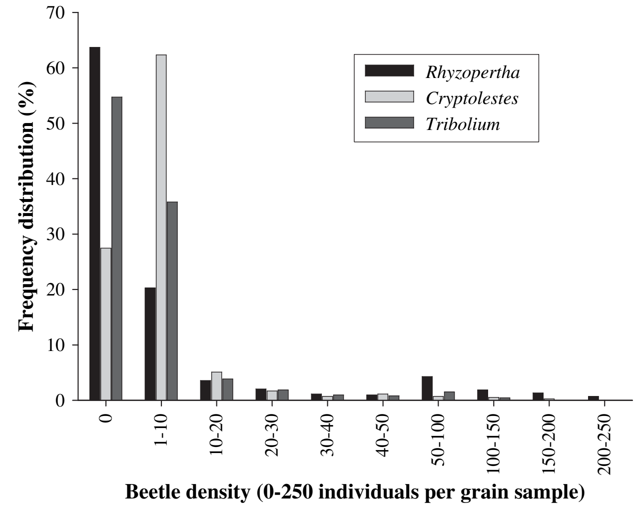

Fig. 1. Frequency distribution of beetle counts in grain samples from grain elevators in Kansas, USA.

density (around 104 individuals) was predicted when counts of both other species were >100.

Regression surfaces of explanatory beetle densities in lower samples showed that the response slope for *R. dominica* was considerably steeper than in top samples, and predictions of *R. dominica* density did not appear to be negatively associated with counts of *C. ferrugineus* (as was seen in top samples) (Fig. 3a). Highest *R. dominica* numbers were observed when counts of both C. *ferrugineus* and *T. castaneum* were high. Counts of *T. castaneum* in lower samples (Fig. 3b) decreased as *C. ferrugineus* increased (similar to the pattern in top samples), but the association with the other two species appeared to be more extreme (more positive effect of *R. dominica* and more negative effect of *C. ferrugineus*). In fact, the regression analysis of lower samples suggested that *T. castaneum* was absent when counts of *C. ferrugineus* exceeded 55 individuals.

Table 2
Regression coefficients of surface response regression analyses.

Rhyzopertha [*R*]		*Tribolium* [*T*]		*Cryptolestes* [*C*]	
Top samples					
Intercept	2.354	Intercept	3.547	Intercept	5.713
C	0.191	R	−0.056	R	0.379
T	0.126	C	0.265	T	0.473
$C \times C$	−0.006	$R \times R$	0.005	$R \times R$	−0.008
$C \times T$	0.018	$R \times C$	0.011	$R \times T$	0.008
$T \times T$	0.0002	$C \times C$	−0.004	$T \times T$	−0.006
R^2	0.30		0.30		0.13
F	16.11***		16.36***		0.5.45***
Lower samples					
Intercept	3.232	Intercept	1.332	Intercept	2.071
C	−0.224	R	0.081	R	0.080
T	1.166	C	0.250	T	0.141
$C \times C$	0.007	$R \times R$	0.001	$R \times R$	−0.001
$C \times T$	0.050	$R \times C$	0.012	$R \times T$	0.001
$T \times T$	−0.012	$C \times C$	−0.009	$T \times T$	−0.002
R^2	0.20		0.18		0.04
F	42.56***		37.99***		6.85***

First, third and fifth columns denote linear and quadratic contributions of *Rhyzopertha* [*R*], *Tribolium* [*T*], and *Cryptolestes* [*C*], and columns two, four and six contain coefficients for each of the three regression analyses at each of two depths with "top samples" = grain samples collected within 2.4 m from the surface in grain silos, and "lower samples" = grain samples collected at least 2.4 m below the surface in grain silos. "R^2" denotes the coefficient of determination, and "F" denotes the F-value with corresponding significance level: "***" indicates $P < 0.001$.

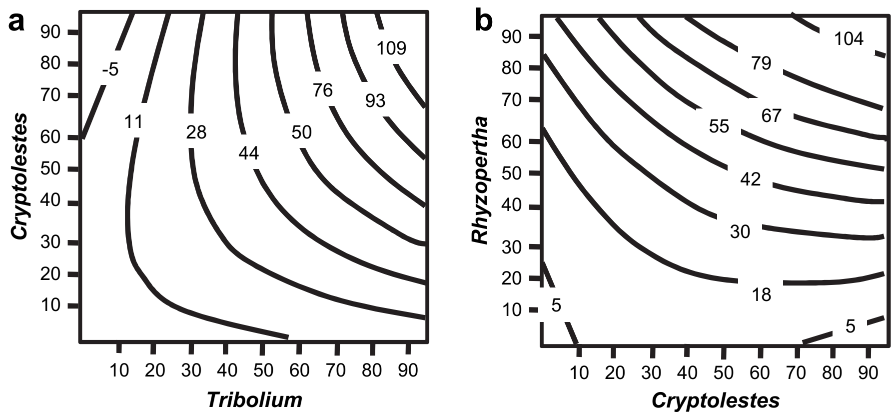

Fig. 2. Response surface of counts of *Rhyzopertha dominica* (a) and *Tribolium castaneum* (b) in top grain samples (0–120 cm below the grain surface). Model parameters are presented in Table 2.

Summarizing the pairwise comparisons of beetle associations (Fig. 4): 1) the two secondary stored-grain pests, *C. ferrugineus* and *T. castaneum*, appeared to have different influence on one another and also showed differences in response to the presence of *R. dominica*. While counts of *C. ferrugineus* were only loosely associated with those of the other two species, *T. castaneum* appeared to be negatively affected by the presence of *C. ferrugineus* (especially in lower samples), while it was positively affected by *R. dominica* in both top and lower samples. The primary granivore, *R. dominica*, was negatively affected by *C. ferrugineus* in top samples, while *C. ferrugineus* and *T. castaneum* were positively associated with counts of *R. dominica* in lower samples.

4. Discussion

Traditionally, unprocessed cereal commodity prices have been fairly low and that has been a serious constraint for development and implementation of integrated pest management strategies, because grain elevator managers have had little economic incentive to invest resources in insect pest control. However, the world market value of wheat has more than doubled in recent years, which will lower action thresholds for insect pests (Pedigo and Rice, 2006), so there is a growing need for better understanding of stored-grain pest ecology and how to reduce losses by these pests. An important aspect of improved integrated pest management strategies in stored-grain environments is to increase our insight into basic ecological aspects of insect associations.

The main objective of this study was to use a large field data set and characterize interspecific associations among three important beetle pests. In order to facilitate interpretation of the results, we used a simple analytical approach that only included linear and quadratic responses. Using this approach, we found that: 1) unlimited food notwithstanding, clear density-dependent associations were found and they varied among species and to some extent between top and lower grain samples, 2) counts of *C. ferrugineus* appeared significantly associated with those of the other two species, 3) >30% of variability of counts of *R. dominica* and *T. castaneum* in top samples could be explained by counts of other two beetles species, and 4) although less variance was explained in counts from lower samples, counts of *R. dominica* and *T. castaneum* were clearly associated with those of the two other beetle species.

One important challenge in our analytical approach is that it will be difficult to categorically document that the density of one beetle species is high or low due to the effect of another species, because of feed-back interactions between species. Similarly, it will be difficult definitively to demonstrate that the density of one beetle species is due to the presence or density of another species in a commercial grain store, because of feed-back interactions between species. In addition, grain temperature, moisture content and other grain quality data were not available for these grain samples. Such variables are likely to be of considerable importance when determining relative abundance of each beetle species in grain samples. In other words, our analysis of beetle "associations" does not suggest that the density of one beetle species is exclusively determined by that of another

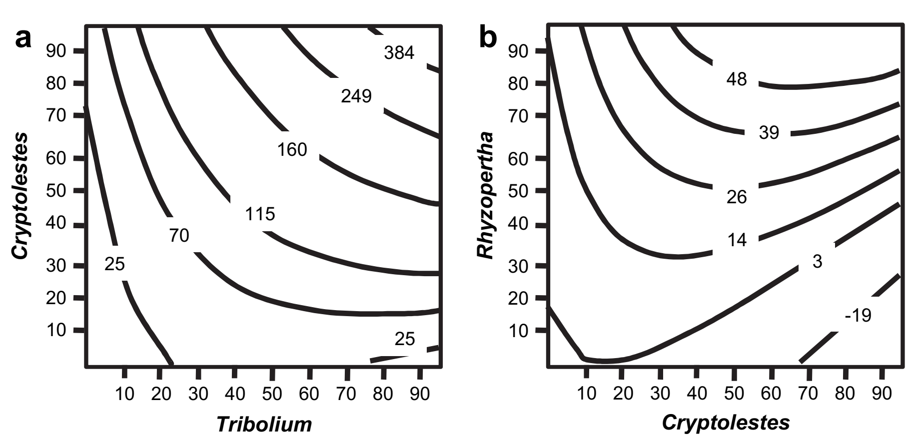

Fig. 3. Response surface of counts of *Rhyzopertha dominica* (a) and *Tribolium castaneum* (b) in lower grain samples (120–240 cm below the grain surface). Model parameters are presented in Table 2.

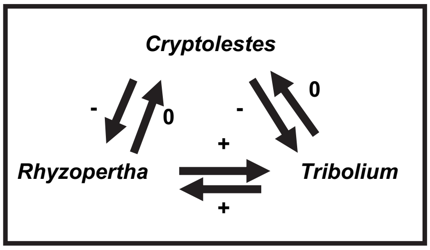

Fig. 4. Summary of relative associations among three stored-grain beetle species.

species, as many grain quality factors and micro-environmental conditions likely play a much larger role than presence/absence of other beetle species. But if presence/absence of one beetle species had no impact on another species, then one would expect a random association, and this analysis clearly showed that all three species appeared to have non-random associations. In fact, our analysis suggested that understanding of 'food availability' and/or 'host suitability' of stored grain may be too simplistic if only defined by the most basic parameters like quantity, temperature and moisture content. It appears that more research is needed to examine, for instance, the association between *T. castaneum* and *C. ferrugineus*, because how can this association of two species on the same trophic level have a negative influence on *T. castaneum* and at the same time have negligible effect on *C. ferrugineus*? In other words, what part of *C. ferrugineus*' biology is giving it a competitive advantage over *T. castaneum*? Very few studies (Rilett, 1949; Throne et al., 1995) have been conducted with stored-grain beetles on a kernel-level to demonstrate preference for certain physical and/or biochemical characteristics, and such studies would be needed for a better understanding of how 'food availability' and/or 'host suitability' are perceived by stored-grain beetles.

4.1. Intraspecific associations of stored-grain beetles

Apart from consuming flour, fungi and other organic debris in the grain mass, *Tribolium* species larvae and adults have been found to readily cannibalize eggs and pupae (Park et al., 1965; Sokoloff, 1974; Longstaff, 1995; Benoît et al., 1998), and cannibalism has also been described for *O. surinamensis* (Jacob and Fleming, 1989; Beckett and Evans, 1994). Several studies conducted under controlled laboratory conditions have suggested that dispersal activity of stored-grain beetles is either density-proportional at low densities (constant) (e.g. Hagstrum and Gilbert, 1976) or is directly dependent upon insect densities when densities are two orders of magnitude higher (density-dependent) (e.g. Barrer et al., 1993; Meikle et al., 1998, 1999). In this study, several grain samples contained $>$500 individuals of either *R. dominica* or *C. ferrugineus*, while other grain samples collected from the same silo on the same date contained no beetles. Substantial variation in beetle density among samples collected in close proximity from the same silo corroborates results from other studies (Nansen et al., 2004a) and suggests that, at least for *C. ferrugineus*, crowding did not seem to elicit dispersal. In fact, one could even argue that the current data would support hypotheses and execution of controlled experiments investigating the possible benefits and behavioral responses of individuals to gregarious beetle communities in stored grain.

4.2. Interspecific associations among stored-grain beetles

Predative associations, with either one species feeding on another or both species feeding on each other, may occur in grain silos, and predation among stored-grain beetles on the same trophic level has been described extensively in laboratory experiments (Lefkovitch, 1968; Sokoloff, 1974; Ciesielska, 1975; LeCato, 1975; Suresh et al., 2001; Hulasare et al., 2005). We demonstrated that stored-grain beetles appeared to affect each other in different ways and that the associations were highly density-dependent. *Cryptolestes ferrugineus* does not require kernels damaged by primary granivores to develop in the grain; this species is able to use hairline cracks in the seed coat that are caused by harvesting equipment to gain access to the wheat germ (Flinn et al., 1993). Thus, it is not surprising that counts of *C. ferrugineus* were only loosely associated with those of *R. dominica*. On the other hand, counts of *C. ferrugineus* appeared to have a progressively negative effect on the density of *R. dominica*, particularly in top samples (where *C. ferrugineus* is predominant) and when counts of *T. castaneum* were low. Counts of *C. ferrugineus* were not significantly affected by those of *T. castaneum*, while there was a clear indication of the opposite. If we assume that *C. ferrugineus* preys on *T. castaneum*, then a possible explanation is that *C. ferrugineus* immatures develop inside damaged kernels and they may therefore be somewhat protected from predation by *T. castaneum*. On the other hand, *T. castaneum* larvae develop outside grain kernels and are therefore more vulnerable to predation by *C. ferrugineus*. However, if the association between *T. castaneum* and *C. ferrugineus* is driven by mutual predation and it is assumed that *T. castaneum* has a competitive disadvantage, then there should be a positive effect of *T. castaneum* on *C. ferrugineus*, and that was not observed. Another explanation is therefore that some type of interference competition is taking place, in which *C. ferrugineus* is suppressing/preventing establishment of *T. castaneum*. We showed indications of a positive association between *R. dominica* and *T. castaneum*, as both species responded positively to the presence of each other. This association between *R. dominica* and *T. castaneum* may be caused by both species showing similar preferences regarding micro-habitat conditions, as *R. dominica* lives inside kernels and *T. castaneum* outside.

Several studies based on laboratory experiments have suggested that interspecific associations are important when examining stored-grain insect communities, and most of these studies have focussed on competition/predation (i.e. Sokoloff, 1974; LeCato, 1975). Suresh et al. (2001) showed that *C. ferrugineus* adults prey on *T. castaneum* eggs, larvae, and pupae. Lefkovitch (1968) reported that *C. ferrugineus* reduced populations of *T. castaneum*. Ordination techniques have been used to examine associations/disassociations among insects, mites and fungi in stored-grain ecosystems (Sinha et al., 1969b, 1979). White and Sinha (1980) conducted principal component analysis of insect counts of *T. castaneum*, *R. dominica*, *S. oryzae*, *C. ferrugineus*, and *O. surinamensis* from experimentally infested grain bins and they showed that, even in experimental storage facilities with low species diversity, there was a tendency for spatial segregation of some species while others tended to co-exist. Two important studies on interspecific associations among stored-grain beetles were conducted by Ciesielska (1975) and Lefkovitch (1968). Both studies were conducted under laboratory conditions in small food containers and constant abiotic regimes, and food availability was likely a constraint in both studies, so the findings are not directly comparable to the present study.

5. Implications of this study

Statistical and simulation modeling have been used extensively to describe insect pest population dynamics in storage facilities (Hagstrum and Throne, 1989; Flinn and Hagstrum, 1990; Meikle et al., 1998, 1999; Mani et al., 2001; Flinn et al., 2003, 2004a,b), and in general, such models have not taken interspecific associations into account. The main justifications for not including interspecific associations in models of stored-product pests have been that dynamics of moths (Bell, 1975; Subramanyam and Hagstrum, 1993) and beetles (Hagstrum and Milliken, 1988; Jacob and Fleming, 1989; Throne, 1994) populations are believed to be driven mainly by temperature and moisture content. It should be mentioned that only three beetle species were examined in this study and that some additional insects, including natural enemies, at low densities were ignored. In cases where such additional insects are found in high numbers they could conceivably have an impact as well. Our study suggests that better understanding of interspecific associations among stored-grain insects may: 1) be used to improve existing computer simulation of population dynamics, 2) provide a platform for more elaborate population model efforts in which outputs encompass density predictions of several beetle species instead of investigating individual species separately, and 3) provide valuable insight into new ecological aspects of the stored-grain ecosystems (Sinha et al., 1969a) – for instance, in studies of biological control of stored-grain beetles (Flinn, 1991, 1998; Flinn et al., 1996) it is important to have detailed insight into the host population density over time. For instance, will natural enemies for control of, for instance *R. dominica*, be competing with *C. ferrugineus*? If *C. ferrugineus* appears to impose the most adverse effect on *R. dominica* in top samples, will natural enemies be able to provide sufficient control further down into the grain mass? These kinds of questions should be asked as part of a holistic ecological approach to research on biological control of stored-product pests. The analysis presented here highlights important short-comings in our current knowledge about the ecology of stored-grain insects and that the regression surfaces may serve as a framework for such ecological population studies.

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