SURVIVAL AND MULTIPLICATION OF STORED-PRODUCT BEETLES AT SIMULATED AND ACTUAL WINTER TEMPERATURES[1]

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Abstract

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Cryptolestes ferrugineus (Stephens), *Cryptolestes pusillus* (Schönherr), *Tribolium castaneum* (Herbst), and *Rhyzopertha dominica* (Fabricius) were gradually exposed to falling temperatures in the laboratory, simulating conditions in the centre of a 12- or 6-m-diameter granary containing wheat. Two years of overwintering mortality for *C. ferrugineus* and *R. dominica* were obtained from 11–13 farm granaries (40–100 t wheat). *Cryptolestes ferrugineus* (adults) was the most cold hardy species among the beetles tested. In the laboratory, survival was 40% at 25°C declining to 10°C over 10 months, whereas at 25°C declining to 0°C over 10 months survival was 7%. *Cryptolestes pusillus* and *T. castaneum* did not survive once temperatures were below 10°C, and *R. dominica* adults did not survive temperatures below 3°C. In the field, there was no survival of *C. ferrugineus* in granaries that had February temperatures of –6.7°C or lower. Six-week exposure to –10°C killed most *C. ferrugineus* adults taken from granaries in February. *Cryptolestes ferrugineus* caught in granaries were more cold hardy than laboratory-reared strains. No *T. castaneum* or *R. dominica* survived an entire winter in granaries in the 2 years tested. Although *C. pusillus* was not tested in the granaries, it is unlikely it could survive the winter, as it had the same level of cold tolerance as *T. castaneum* in the laboratory. The implications for the population dynamics of these pest species in prairie grain are discussed.

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Résumé

Cryptolestes ferrugineus (Stephens), *Cryptolestes pusillus* (Schönherr), *Tribolium castaneum* (Herbst) et *Rhyzopertha dominica* (Fabricius) ont été exposés à des températures progressivement plus froides dans un laboratoire simulant les conditions qui prévalent au centre d'un silo à grains de 12 ou 6 m de diamètre contenant du blé. Les résultats sur la mortalité de *C. ferrugineus* et de *R. dominica* pendant deux hivers ont été obtenus dans 11 à 13 silos à grains (40–100 t de blé). L'espèce *C. ferrugineus* (les adultes) s'est révélée la plus résistante au froid parmi toutes les espèces étudiées. En laboratoire, la survie a été estimée à 40% à une température graduellement descendante de 25 à 10°C en 10 mois, et à 7% à une température graduellement descendante de 25 à 0°C en 10 mois. *Cryptolestes pusillus* et *T. castaneum* n'ont pas survécu aux températures inférieures à 10°C, et les adultes de *R. dominica* n'ont pas survécu aux températures inférieures à 3°C. Sur le terrain, aucun *C. ferrugineus* n'a survécu dans les silos où les températures en février étaient égales ou inférieures à –6,7°C. Une exposition de 6 semaines à une température de –10°C a tué presque tous les adultes de *C. ferrugineus* recueillis dans les silos en février. Les *C. ferrugineus* capturés dans les silos étaient plus résistants au froid que les souches élevées en laboratoire. Aucun *T. castaneum* ou *R. dominica* n'a survécu tout un hiver dans les silos au cours des 2 années de l'étude. Bien que nous n'ayons pas fait de tests sur *C. pusillus* dans les silos, il est peu probable que l'espèce puisse survivre à l'hiver puisque son seuil de tolérance au froid s'est avéré égal à celui de *T. castaneum* en laboratoire. La dynamique des populations de ces espèces dans les silos à grains des prairies est examinée à la lumière de ces résultats.

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Introduction

Frequency of insect infestation in cereals stored on the farm in western Canada varies annually (Madrid et al. 1990), but is always a significant problem throughout the grain industry (Sinha and Watters 1985). The most consistent pest on farms is the rusty grain beetle, *Cryptolestes ferrugineus* (Stephens) (Cucujidae), followed in frequency of occurrence by the red flour beetle, *Tribolium castaneum* (Herbst) (Tenebrionidae) (Madrid et al. 1990). Other grain-feeding insects that occur infrequently in western Canada include the flat grain beetle, *Cryptolestes pusillus* (Schönherr) (Cucujidae) (White et al. 1995), and the lesser grain borer, *Rhyzopertha dominica* (Fabricius) (Bostrichidae) (Fields et al. 1993).

There have been many studies on the cold tolerance of stored-product insects (Fields 1992). For *C. ferrugineus*, adults are the most cold tolerant stage (Smith 1970). They freeze and die between −17 and −20°C (Smith 1970; Fields 1992). Once cold acclimatized in granaries, 50% of the population dies after 40 days at −10°C (Fields 1990). Cold-acclimatizing adults at 15°C for 2 weeks in the laboratory produced populations that had 50% mortality after 11 days at −12°C and after 31 days at −6°C. Of the species that are found in stored grain in western Canada, *C. ferrugineus* is considered the most cold tolerant, *R. dominica* and *C. pusillus* have intermediate cold tolerance, and *T. castaneum* is the least cold tolerant (Fields 1992). However, it is difficult from these studies to predict if these insects can survive winter in western Canada. Fields (1990) did show that *C. ferrugineus* can overwinter in grain in western Canada, but this study was limited to 1 year in one granary and tested only *C. ferrugineus*.

The aim of this study was to determine if the less cold hardy species, *R. dominica*, *C. pusillus*, and *T. castaneum*, found in western Canadian grain, could survive and multiply under temperatures typical of granaries in this region. We approached this question in two ways. In the laboratory, we simulated the decline in temperature over a 10-month period using simulation temperature data for granaries that are 12 or 6 m in diameter (Muir 1973; Jayas et al. 1994) and measured survival and offspring production of the four species found in western Canada. We placed *C. ferrugineus* and *R. dominica* in several granaries during two winters to estimate overwintering survival.

Materials and Methods

Laboratory. Adults of *T. castaneum*, *C. ferrugineus*, and *C. pusillus* were originally collected from farms in Manitoba in 1991, 1990, and 1985, respectively. Adults of *R. dominica* were collected from a farm in Alberta in 1992. All were cultured in the laboratory at 30 ± 1°C and 70 ± 5% RH on whole wheat (*R. dominica*), whole wheat plus wheat germ (*Cryptolestes* spp.), or wheat flour plus brewer's yeast (*T. castaneum*). Eggs of all species were collected by placing adults on wheat flour plus brewer's yeast at 30 ± 1°C and 70 ± 5% RH for 24 h and then sifting the flour. Immatures of *T. castaneum* and *R. dominica* were mass reared at these conditions on this food and sex was determined in the pupal stage (Halstead 1963). Eggs of *Cryptolestes* spp. were placed individually in gelatin capsules (size 00, 2.5 cm long × 0.8 cm diameter) on ground wheat and reared under the same conditions, and sex was determined when adults were newly emerged (Rilett 1949; White and Bell 1990). Eighty adults (two females and two males per vial) of each species were placed in 20 vials (7 cm high × 2.9 cm diameter) on 8 g ground wheat in an incubator at 25 ± 1°C and 75 ± 5% RH. The same number of insects were placed in vials in another growth chamber at the same initial conditions. Temperature regime in one chamber simulated that in a 12-m-diameter grain bulk (25–10°C) and that in the other chamber that in a 6-m-diameter grain bulk (25–0°C) (Tables 1 and 2). These temperatures were obtained from a model that simulates changes in temperatures at the centre of a grain mass during winter (Jayas et al. 1994). Every 4 weeks, all adult insects were removed from the ground grain with a fine brush after spreading the food in a tray, survival was determined, and live adults were placed on new food and returned to the new temperature for 4 weeks. The old food was placed on wheat in Berlese funnels for 24 h and larvae collected and counted (Canadian Grain Commission 1992). This was done over 40 weeks, after which surviving adults were placed on new food and returned to 25°C for 4 weeks, to simulate a return to summer temperatures.

Granaries. To obtain young adults of *C. ferrugineus* and *R. dominica* for overwintering experiments in granaries, cultures were sieved to remove old adults, held at 30 ± 1°C and 70 ± 5% RH, and sieved a second time 3 weeks later to obtain young adults. After an additional week at 30°C, adults were placed in ventilated plastic vials (3 cm diameter × 5 cm long, 100 adults per vial, except 50 *C. ferrugineus* per vial were used in 1991–1992) with 20 g wheat (5% cracked). The vials were in turn placed in polyvinylchloride pipes drilled with holes for ventilation (4 cm diameter × 18 cm long, 6 vials per pipe) which were packed with wheat taken from the granary in which they were placed. The pipes were held at 15°C for 8–10 days before being pushed 1 m down into the top surface of 11 or 13 granaries, on 15 November 1990 or 5–6 November 1991. The granaries varied in capacity from 40 to 100 t (Tables 3 and 4). For *R. dominica*, immatures were also tested for overwintering survival, as they were more cold hardy than adults (David et al. 1977).

To obtain immatures of *R. dominica*, 400 adults were placed on wheat and held at 30°C; adults were sieved off 3 weeks later. The grain with these immature insects was placed into vials and treated similarly to those with the adults. Therefore, as the pipes were placed into the granaries *R. dominica* were either larvae or pupae (Birch 1945). To estimate the number of immature individuals in the grain, 12 vials were held at 30°C for 5 weeks, and all adults that had developed were removed by sieving the vial contents three times.

In 1990–1991, the culture of *C. ferrugineus* had been reared in the laboratory for over 10 years; in 1991–1992 the same culture was used and in three granaries a culture that had been in the laboratory for a few months was also used. For *R. dominica*, cultures were started from adults collected from the field using pheromone-baited multiple funnel traps (Fields et al. 1993) the summer of the test.

For most of the granaries, pipes containing the insects were removed on 4 February 1991 or 3 February 1992. A second sample was removed from the granaries from 18 March to 25 May in 1991 and on 24 February (one site) or 13 April in 1992. In 1991, all pipes were removed in December from two granaries, because the wheat was sold by the farmer earlier than expected. Once the pipes were removed from the granary, three vials were held at 5°C for 1 day and 30°C for 4 h before counting the number of live and dead adults. The remaining three vials were used to estimate the cold tolerance of *C. ferrugineus*. The vials were placed at −10°C, a vial was removed after 2, 4, and 6 weeks, and the mortality assessed. For adults and immatures of *R. dominica*, all six vials were warmed immediately and mortality assessed. Larval numbers were assessed by incubating the grain at 30°C for 4 weeks and counting emerged adults. Many of the granaries had natural infestations of *C. ferrugineus*, and some of these insects were found in the pipes. The wheat in the pipes was sieved (three pipes per granary per date), and the number of live and dead insects was counted to estimate the survival in natural populations.

Granaries were located on farms in southern Manitoba. They were filled with 40–100 tonnes of wheat harvested in August or September. Each year, there were three welded hopper bottom granaries, the rest were circular bolted steel granaries. In each granary, a thermocouple was attached to one of the pipes and the temperature was measured once a week. The moisture content of the wheat in the pipes was measured using a dielectric moisture meter (model 919, Labtronics, Winnipeg, MB) after they were removed from the granaries and sieved for insects. Mean monthly air temperatures near Winnipeg were obtained from Atmospheric Environment Service, Environment Canada, Winnipeg, MB.

TABLE 1. Number of stored-product beetle adults surviving per vial (two males and two females per vial) and larvae produced per vial on ground wheat at temperatures that simulate those in a 12-m-diameter grain bulk

Sample count (week)	Temp. (°C)	Temp. Period (weeks)	*Cryptolestes ferrugineus*		*Cryptolestes pusillus*		*Tribolium castaneum*		*Rhyzopertha dominica*	
			Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae
0	25		4.0 ± 0		4.0 ± 0		4.0 ± 0		4.0 ± 0	
4	25	0–4	4.0 ± 0	59.0 ± 7.0	4.0 ± 0	94.1 ± 8.0	4.0 ± 0	163.9 ± 8.9	3.6 ± 0.2	96.5 ± 6.9
8	23	4–8	4.0 ± 0	62.0 ± 5.6	4.0 ± 0	62.0 ± 7.0	4.0 ± 0	168.9 ± 7.0	3.6 ± 0.2	38.7 ± 6.2
12	22	8–12	3.9 ± 1	34.3 ± 4.3	3.5 ± 0.2	34.0 ± 6.4	3.5 ± 0.2	69.9 ± 8.0	3.3 ± 0.2	38.3 ± 6.7
16	20	12–16	3.9 ± 0.1	18.1 ± 4.9	3.5 ± 0.2	18.9 ± 4.8	3.5 ± 0.2	30.7 ± 5.8	2.2 ± 0.4	11.0 ± 3.5
20	19	16–20	3.9 ± 0.1	9.3 ± 2.4	3.0 ± 0.3	5.4 ± 1.8	3.3 ± 0.2	2.7 ± 0.8	1.1 ± 0.3	0.1 ± 0.1
24	17	20–24	3.8 ± 0.1	0.1 ± 0.1	2.7 ± 0.3	0	3.3 ± 0.2	0	0.5 ± 0.2	0
28	15	24–28	3.7 ± 0.2	0	1.8 ± 0.3	0	2.6 ± 0.3	0	0.1 ± 0.1	0
32	13	28–32	3.7 ± 0.2	0	0.6 ± 0.2	0	1.2 ± 0.4	0	0	0
36	12	32–36	3.6 ± 0.2	0	0.1 ± 0.1	0	0.1 ± 0.1	0	0	0
40	10	36–40	3.1 ± 0.3	0	0	0	0	0	0	0
44	25	40–44	1.6 ± 0.3	12.5 ± 3.6	0	0	0	0	0	0

NOTE: Values in the table are means ± SE; $n = 20$ vials per species.

TABLE 2. Number of stored-product beetle adults surviving per vial (two males and two females per vial) and offspring produced per vial on ground wheat at temperatures that simulate those in a 6-m-diameter grain bulk

Sample count (week)	Temp. (°C)	Temp. period (weeks)	*Cryptolestes ferrugineus*		*Cryptolestes pusillus*		*Tribolium castaneum*		*Rhyzopertha dominica*	
			Adults	Larvae	Adults	Larvae	Adults	Larvae	Adults	Larvae
0	25		4.0 ± 0		4.0 ± 0		4.0 ± 0		4.0 ± 0	
4	25	0–4	4.0 ± 0	73.3 ± 9.6	4.0 ± 0	60.0 ± 0.1	4.0 ± 0	184.6 ± 9.5	3.8 ± 0.2	45.9 ± 2.7
8	22	4–8	4.0 ± 0	124.2 ± 6.1	4.0 ± 0	5.8 ± 1.2	4.0 ± 0	162.0 ± 3.6	3.8 ± 0.1	53.1 ± 6.0
12	20	8–12	4.0 ± 0	30.2 ± 3.8	3.6 ± 0.2	24.2 ± 3.2	4.0 ± 0	119.5 ± 13.5	3.6 ± 0.2	38.7 ± 5.1
16	16	12–16	4.0 ± 0	0	3.6 ± 0.2	0.9 ± 0.3	3.7 ± 0.2	0.8 ± 0.2	3.0 ± 0.3	0
20	14	16–20	4.0 ± 0	0	3.0 ± 0.4	0	3.5 ± 0.2	0	2.7 ± 0.3	0
24	11	20–24	3.9 ± 0.1	0	0.7 ± 0.3	0	0.9 ± 0.4	0	2.3 ± 0.4	0
28	8	24–28	3.9 ± 0.1	0	0	0	0	0	1.7 ± 0.4	0
32	5	28–32	3.5 ± 0.2	0	0	0	0	0	0.1 ± 0.1	0
36	3	32–36	2.4 ± 0.4	0	0	0	0	0	0	0
40	0	36–40	0.6 ± 0.3	0	0	0	0	0	0	0
44	25	40–44	0.2 ± 0.1	3.0 ± 1.1	0	0	0	0	0	0

NOTE: Values in the table are means ± SE; $n = 20$ vials per species.

Results

Laboratory. At 25°C declining to 10°C, only *C. ferrugineus* survived to the end of 40 weeks (Table 1), with 13 females and 11 males surviving (mean of 1.6 adults per vial). When returned to 25°C, 19.2 ± 1.4 larvae per female (249 larvae in 20 vials, 12.5 ± 3.6 larvae per vial, Table 1) were produced compared with 29.5 ± 2.4 larvae per female initially ($n = 40$ females, about 1180 larvae in 20 vials, 59.0 ± 7.0 larvae per vial, Table 1) at 25°C. No adults of either *C. pusillus* or *T. castaneum* survived for 40 weeks once at 10°C, and no adults of *R. dominica* survived for 32 weeks once at 13°C. All offspring production essentially stopped at and below 17°C.

At 25°C declining to 0°C, only *C. ferrugineus* survived to the end of 40 weeks (Table 2). There was 93% mortality, with only three females surviving. When returned to 25°C they produced 20.0 ± 2.7 larvae per female (60 larvae in 20 vials) compared with 36.0 ± 4.8 larvae per female initially ($n = 40$ females, about 1440 larvae in 20 vials). *Cryptolestes pusillus* and *T. castaneum* did not survive for 24 weeks once at 11°C; some adults of *R. dominica* survived for 32 weeks until at 5°C. Offspring production for *C. ferrugineus* and *R. dominica* ceased at 16°C; for *C. pusillus* and *T. castaneum* it ceased at 14°C.

Granaries. The estimated rate of temperature decline in unventilated granaries was from 0.10 to 0.26°C/day, or approximately 1°C every 4–10 days (estimation of slope; Figs. 1, 2; Tables 3, 4). The monthly mean temperatures were lower in 1991–1990 than in 1991–1992 except for February and March (Figs. 1, 2; $p < 0.05$, t test). This caused lower minimum grain temperatures in 1990–1991 than in 1991–1992 (–8.5 ± 0.7 vs. –5.5 ± 0.7, $p = 0.007$, t test, $t_{df} = 17$; aerated granaries were excluded from the analysis). The mean date of minimum grain temperature was later in 1990–1991 than in 1991–1992 (20 March 1991 vs. 8 March 1992, SEM ± 2 days, $p = 0.0001$, t test, $t_{df} = 17$). In the granaries that were monitored until June 1991, the temperatures at 1 m in the grain centre had not risen above the developmental threshold (15°C), but the temperatures had risen above the threshold (5°C) for movement. In the two granaries that were aerated by fans (distinguishable by the rapid fall in temperature, Fig. 1), minimum temperatures were approximately –15°C. Grain moisture content varied from 12.8 to 15.8% in 1990–1991 and from 10.8 to 14.7% in 1991–1992 (Tables 3, 4).

Laboratory-reared *C. ferrugineus* did not survive in granaries that had a temperature of –6.7°C or lower on February 1991 (Table 3). In the following winter, all granaries had temperatures greater than –6.3°C on 3 February 1992, and some *C. ferrugineus* survived in all of the granaries (Table 4). In general, the lower the temperature, the lower the survival. Six weeks at –10°C in the laboratory eliminates most of the survivors taken from granaries in February. In all but one case, wild *C. ferrugineus* taken from the pipes had higher survival than laboratory-reared *C. ferrugineus* insects held in vials. No laboratory-reared *C. ferrugineus* survived when removed at dates subsequent to early February, but some wild *C. ferrugineus* survived until mid-April. All wild *C. ferrugineus* were dead in only one instance (Table 2).

In 1991–1992, in three granaries *C. ferrugineus* from a culture maintained in the laboratory for over 10 years were compared to insects that had been recently collected from the field, less than 1 year in the laboratory. In one granary, survival of the laboratory strain was higher than that of the field strain (29 ± 1 vs. 14 ± 2%, t test, $p = 0.005$, $t_{df} = 4$), and in the other two granaries there were no significant differences (laboratory vs. field: 26 ± 8 vs. 31 ± 8%, $p = 0.41$, $t_{df} = 4$; 21 ± 2 vs. 13 ± 6%, $p = 0.25$, $t_{df} = 4$).

Some *R. dominica* survived until February in both years, but survival was rare below –2°C (Tables 3, 4). As with the laboratory-reared *C. ferrugineus*, no *R. dominica* were alive in samples taken after February. In the two winters, two or three granaries were also infested with *T. castaneum*, but by early February all were dead, although the *C. ferrugineus* caught in the same pipes had 59–93% survival.

TABLE 3. Percent survival (mean ± SE) of insects held in 13 granaries from 15 November 1990 until 4 February or 18 March 1991

Temp. (°C)					*Cryptolestes ferrugineus*						*Rhyzopertha dominica*	
					Wild		Laboratory reared					
								At −10°C for				
4 Feb.	18 Mar.	Temp. decline (°C/day)[a]	Grain moisture content (%)	Size of wheat bulk (t)	4 Feb.	18 Mar.	4 Feb.	2 weeks	4 weeks	6 weeks	Adult (Feb. 4)	Immature (Feb. 4)
2.0	−15.4	0.18 ± 0.01	15.0 ± 0.2	80	98 ± 1	78 ± 1	31 ± 5	16	10	3	61 ± 3	60 ± 5
−1.0	—	0.23 ± 0.02	12.8 ± 0.1	60	97 ± 3	—	35 ± 6	4	1	0	13 ± 9	58 ± 5
−2.5	−7.1	0.23 ± 0.01	13.9 ± 0.1	80	78 ± 5	37 ± 6	73 ± 1	29	8	0	2 ± 1	0.9 ± 0.1
−2.6	−7.3	0.21 ± 0.01	13.7 ± 0.1	40	—	—	53 ± 5	25	0	0	0 ± 0	0.2 ± 0.2
−3.3	−8.4	0.17 ± 0.01	13.9 ± 0.1	60[b]	85 ± 4	—	24 ± 3	15	7	0	0 ± 0	0 ± 0
−5.0	—	0.22 ± 0.01	12.8 ± 0.3	100	88 ± 4	—	23 ± 1	5	0	0	0 ± 0	0 ± 0
−5.1	−9.6	0.25 ± 0.01	15.1 ± 0.1	60[b]	95 ± 3	40 ± 6[c]	63 ± 2	16	6	0	0.5 ± 0.3	0.4 ± 0.2
−5.3	−7.0	0.26 ± 0.01	14.5 ± 0.2	80	59 ± 15	50 ± 1[d]	68 ± 3	41	20	4	0 ± 0	0.1 ± 0.1
−5.9	−10.2	0.19 ± 0.03	14.8 ± 0.1	60	—	—	6 ± 1	1	0	0	0 ± 0	0 ± 0
−6.7	−8.1	0.10 ± 0.01	15.8 ± 0.1	80	—	—	0 ± 0	—	—	—	0 ± 0	0 ± 0
−8.2	−10.6	0.23 ± 0.01	14.8 ± 0.1	60[b]	—	—	0 ± 0	—	—	—	0 ± 0	0 ± 0
−8.9	−11.9	0.25 ± 0.01	13.0 ± 0.1	60	—	—	2 ± 0	0	0	0	0 ± 0	0 ± 0
−14.3	−13.6	0.33 ± 0.08[e]	15.0 ± 0.2	95	—	—	0 ± 0	—	—	—	0 ± 0	0 ± 0

NOTE: Once taken from granaries, *C. ferrugineus* from laboratory cultures were divided into four groups, with immediate survival assessment, or assessment after being held at −10°C for 2, 4, or 6 weeks. In granaries, wild *C. ferrugineus* were found in the pipes (10–3422) used to hold the vials that held laboratory-reared *C. ferrugineus* and *R. dominica*.

[a] Estimation of slope from Fig. 1.

[b] Hopper-bottomed granaries.

[c] Survival of wild *C. ferrugineus* 0 ± 0% on 27 May.

[d] Survival of wild *C. ferrugineus* 39 ± 1% on 8 April.

[e] Aeration turned on for several days in December.

TABLE 4. Percent survival (mean ± SE) of insects held in 11 granaries from 5 November until 23 December 1991 for samples above 0°C or 3 February 1992 for samples below 0°C

				Cryptolestes ferrugineus					*Rhyzopertha dominica*	
					Laboratory reared					
						At −10°C for				
Temp. on 3 Feb. (°C)	Temp. decline (±SEM, °C/day)[a]	Grain moisture content (%)	Size of wheat bulk (*t*)	Wild	3 Feb.	2 weeks	4 weeks	6 weeks	Adult (3 Feb.)	Immature (3 Feb.)
15	0	12.7 ± 0.1	—[b]	—	43 ± 3	26	6	1	34 ± 11	50 ± 5
9.1	0.24 ± 0.01	13.5 ± 0.6	80	—	42 ± 2	38	2	0	82 ± 8	—
5.5	0.26 ± 0.01	11.4 ± 0.1	80	—	30 ± 2	—	—	—	81 ± 7	75 ± 6
−0.6	0.27 ± 0.01	12.6 ± 0.1	80	92 ± 62[c]	21 ± 2	0	4	2	6 ± 3	35 ± 13
−1.0	0.25 ± 0.01	10.8 ± 0.1	80	—	1 ± 1	0	0	0	1 ± 1	13 ± 3
−1.9	0.22 ± 0.01	12.4 ± 0.1	80	33 ± 16	16 ± 4	10	2	0	0 ± 0	0.3 ± 0.3
−2.8	0.25 ± 0.01	14.7 ± 0.3	80	93 ± 2	25 ± 1	2	2	0	0 ± 0	0.3 ± 0.3
−3.9	0.20 ± 0.01	12.7 ± 0.1	40	87 ± 7	26 ± 8	22	12	16	0 ± 0	0.3 ± 0.3
−4.8	0.22 ± 0.02	12.4 ± 0.1	80	—	9 ± 1	0	2	0	0 ± 0	0 ± 0
−5.6	0.23 ± 0.01	13.7 ± 0.1	60[d]	65 ± 16	10 ± 7	28	14	—	0 ± 0	0.8 ± 0.4
−6.2	0.24 ± 0.01	13.6 ± 0.1	60[d]	—	29 ± 1	16	10	6	0 ± 0	0 ± 0
−6.3	0.25 ± 0.01	12.8 ± 0.1	60[d]	—	27 ± 5	24	2	0	0 ± 0	0 ± 0

NOTE: Once taken from granaries, *C. ferrugineus* from laboratory cultures were divided into four groups, with immediate survival assessment, or assessment after being held at −10°C for 2, 4, or 6 weeks. In five granaries, wild *C. ferrugineus* were found in the pipes (4–871) used to hold the vials that held laboratory-reared *C. ferrugineus* and *R. dominica*.
[a] Estimation of slope from Fig. 2.
[b] Laboratory.
[c] Survival of wild *C. ferrugineus* 58 ± 4% on 13 April.
[d] Hopper-bottomed granaries.

Discussion

As seen in other studies (Fields 1992), we found that in both laboratory tests and tests in granaries, *C. ferrugineus* was the most cold hardy, *R. dominica* had intermediate cold tolerance, and *T. castaneum* was the least cold hardy of all insects tested. The only test for which this was not seen was in the laboratory tests when insects were cooled only to 10°C. In that experiment adults of *R. dominica* had shorter longevity than did the other three insects tested. It could be that at these mild temperatures mortality is not caused by cold injury (Fields 1992), but rather by their inability to feed, so death was by starvation or desiccation. We rate *C. pusillus* as having similar cold tolerance to that of *T. castaneum*. There are only a few investigations into the cold tolerance of *C. pusillus* (Williams 1955; Lee et al. 1992). Lee et al. (1992) rated *C. pusillus* as being more cold hardy than *T. castaneum* but less cold hardy than *R. dominica* and *C. ferrugineus*. However, neither of these studies cold acclimatized the insects before testing for cold tolerance. It is important to cold acclimatize insects, because this occurs naturally in granaries in the fall and winter, and because it increases the insect's cold tolerance by approximately 10-fold (Fields 1992).

There are several possible reasons for differences between overwintering survival of the wild and laboratory-reared *C. ferrugineus*. Insects that were caught in the pipe may not be representative of the entire population in the granary. Insects had to move into the pipe, and hence may be more fit and perhaps more cold hardy than the rest of the population. Insects reared in the laboratory were reared under high density (1000–2000 individuals/kg of wheat), whereas even in heavily infested granaries, insect densities rarely exceed 10 insects/kg. In general, the laboratory-reared insects were reared in grain with higher moisture content than the wild-reared insects (16 vs. 11–16%). Although higher moisture content during cold exposure increases cold tolerance (Fields 1990), it is unknown what influence rearing moisture content has on cold tolerance. Finally, because some of the insects used in the granary tests had been reared in the laboratory for over 10 years, they may have lost some of their ability to tolerate cold temperatures. However, our data indicated that there was no difference in overwintering survival by early February between *C. ferrugineus* that had been reared in the laboratory for 1 year and insects that had been reared for over tens of years in the laboratory. It is possible that cold hardiness is rapidly lost in laboratory cultures. In more detailed studies, White and Bell (1993, 1994) examined the fitness of inbred *C. ferrugineus* reared in the laboratory for 15 years at 30°C compared with adults from cultures taken recently from the field. The wild-type strain laid more eggs and had a longer lifespan at 22°C than the inbred strain which had been maintained at 30°C for years. Also, David et al. (1977) demonstrated that recently collected field strains of *Sitophilus granarius* (L.) were more cold hardy than laboratory strains; however, there were no differences between the field and laboratory strains of *Sitophilus oryzae* (L.), and laboratory strains of *R. dominica* were more cold hardy than field strains. Therefore, although it is possible that the differences in overwintering survival we saw were due to selection of non-cold-hardy strains in the laboratory, more study is required to verify this hypothesis.

Our studies indicated that *T. castaneum, R. dominica*, or *C. pusillus* were unable to survive the entire winter in granaries in western Canada. The case is strongest for *T. castaneum*; in five naturally infested granaries all the *T. castaneum* were found dead by February. For *R. dominica*, laboratory-reared insects did not survive the winter in granaries. However, neither did laboratory-reared *C. ferrugineus*, whereas wild populations were able to survive the entire winter. To confirm that *R. dominica* does not overwinter in granaries in western Canada, a study using full granaries artificially infested with *R. dominica* is required. The cold tolerance of *C. pusillus* was not tested in granaries, but in laboratory studies the level of survival was similar to that of *T. castaneum*, and hence we conclude that it is unlikely to be able to overwinter. Because it is unlikely these species are able to overwinter in stored grain in western Canada, they would have to reinfest each year from

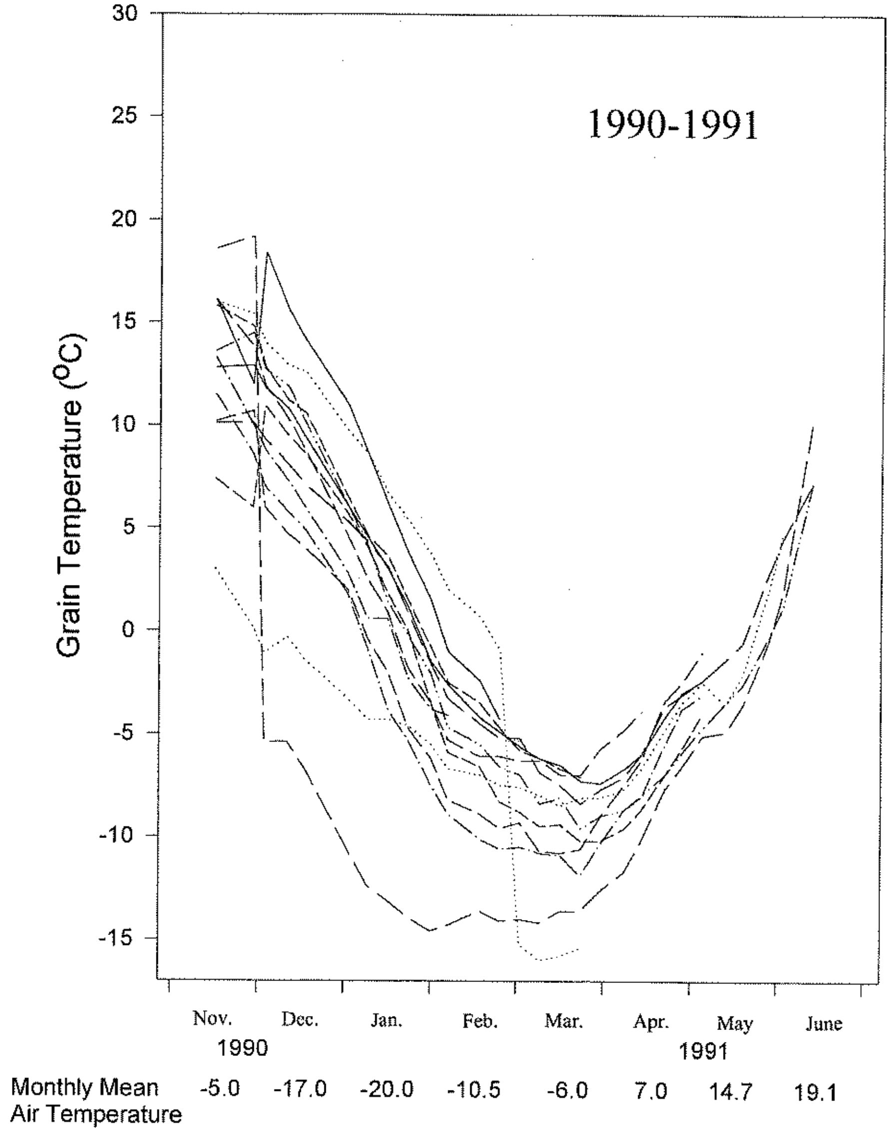

FIG. 1. Temperatures 1 m deep in the centre of 13 wheat bulks during 1990–1991. Rapid decrease in temperature in two granaries reflects aeration of the grain using fans. Mean monthly temperatures (°C) are given.

warm refuges in Canada, such as feed mills (Mills and White 1993), cattle or pig barns, food-processing facilities (Sinha and Watters 1985). Also, they may overwinter in granaries with hot spots caused by metabolic respiration of large populations of insects or mould (Sinha 1961). These species may also fly into Canada from more southerly locations in the United States, as was suggested for *R. dominica* (Fields et al. 1993).

For *C. ferrugineus*, laboratory data predicted that there would be 15–78% survival depending upon the size of the granary. None of the laboratory-reared insects survived the entire winter in granaries, but in the two infested granaries that we were able to follow until April there was a similar level of survival, i.e. 39 and 58%. The overwintering survival would

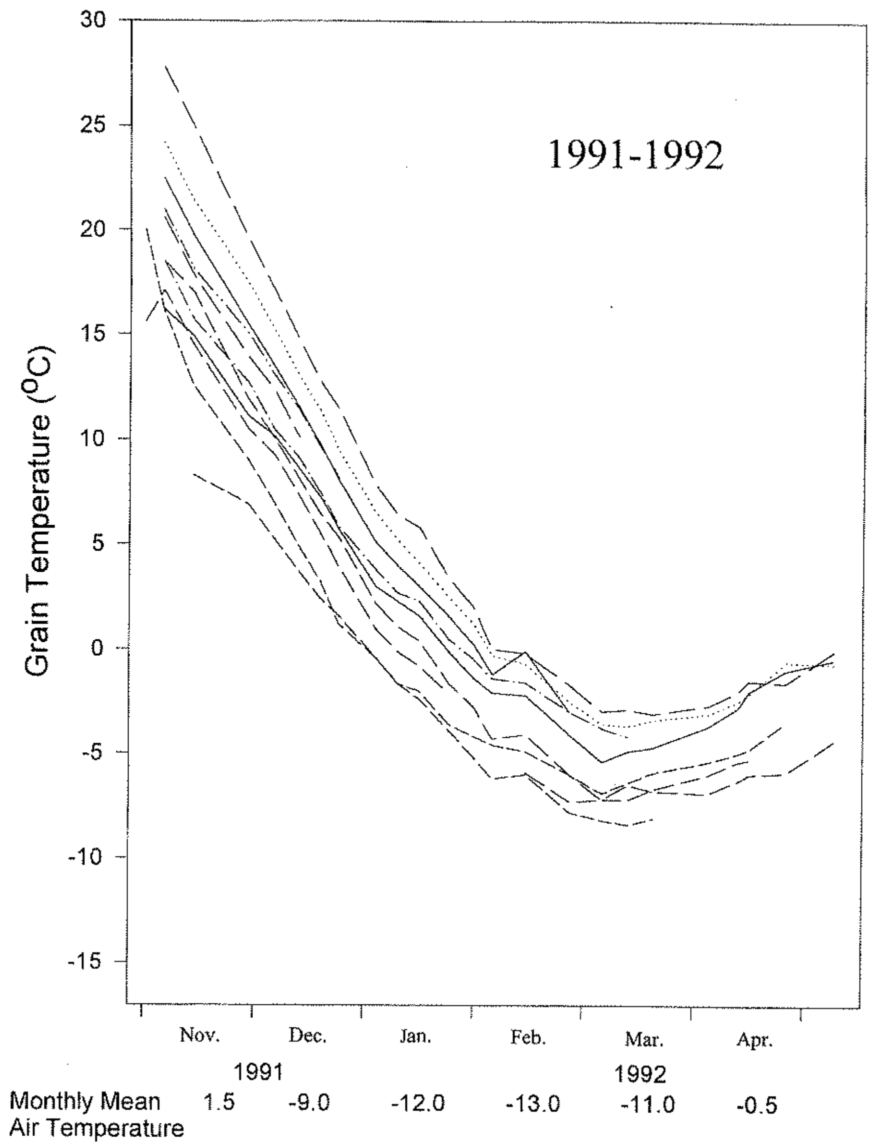

FIG. 2. Temperatures 1 m deep in the centre of 11 wheat bulks during 1991–1992. Mean monthly temperatures (°C) are given.

of course vary from year to year and from granary to granary. If the *T. castaneum*, *R. dominica*, and *C. pusillus* migrate from warm refuges within Canada, or from the United States, this may also be true for *C. ferrugineus*. Therefore *C. ferrugineus* populations in the early summer could be a mix of immigrants and resident insects that have survived the winter.

Cryptolestes ferrugineus is one of the more cold hardy stored-product insect pests. However, cold tolerance is not an absolute necessity, as *T. castaneum* is one of the least cold tolerant stored-product insects, and yet is a common pest of stored grain in western Canada. Growth rate may be a more important factor than cold tolerance in determining if an insect will become a pest in stored grain in western Canada, as there is only a short period after harvest when stored grain is warm enough for growth. *Cryptolestes ferrugineus* and *T. castaneum* have the highest rates of population increase for stored-product beetles, i.e. 60- to 70-fold per month, whereas *S. granarius, R. dominica,* and *C. pusillus,* which are as or more cold hardy than *T. castaneum,* have a rate of population increase of only 10- to 20-fold per month (Howe 1965; Sinha and Watters 1985). To control *C. ferrugineus,* the grain must be cooled by ventilation during the winter to bring it below −10°C for several weeks.

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