



Survival and reproduction of lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) on flora associated with native habitats in Kansas

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ABSTRACT

Capture of *Rhyzopertha dominica* in pheromone-baited traps located many kilometers away from grain storage suggests that this species may be exploiting non-grain food sources. To investigate the potential for survival of this species on alternative hosts in the absence of grain, we conducted no-choice feeding assays with twigs and seeds of trees, and seeds of grasses, forbs, and shrubs, commonly encountered on Kansas prairie landscapes where *R. dominica* has been captured. In addition, *R. dominica* development and progeny production were assessed on seeds that adults were able to survive on for at least two weeks. Adult survival was poor on grass and forb seeds, although 13.4% of individuals survived on *Elymus canadensis*, Canada wildrye, seeds after two weeks, compared with 80.3% on *Triticum aestivum*, wheat, and 0.0% survival in the absence of food. Beetles readily tunneled into twigs from a wide range of tree species, but survival was generally low. A few individuals survived up to four weeks on *Gleditsia triacanthos*, honey locust. In contrast, bioassays showed that *R. dominica* could survive and reproduce on damaged seeds (acorns) of six species of oak, but not on undamaged seeds. For example, survival was 95.8% on damaged *Quercus muehlenbergii*, chinquapin oak. A survey of acorns at the original field collection site showed that the majority of the acorns on the ground had been cracked or bored into by insects and small mammals. Furthermore, we recovered three *R. dominica* adults from acorns collected in the field and held in sealed containers in the laboratory. These findings suggest that *R. dominica* populations in Kansas can persist on wild acorns when grain is not available.

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1. Introduction

Lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), is hypothesized to have originated in tropical regions of the Indian subcontinent, originally as a wood borer, before expanding its host range to small grains. It is now a cosmopolitan species, occurring in all areas of the world where grain is produced and stored (Potter, 1935; Crombie, 1941). *Rhyzopertha dominica* was first documented in the USA about one century ago (Tucker, 1909). This species is a major pest of stored grain because it feeds on whole grain in both the larval and adult life stages and produces insect damaged kernels (IDK), which are a measure of infestation used in grading of grain. Females deposit eggs loosely on the outside of grain kernels and the first instars tunnel into kernels where they complete

development. Development from egg to adult requires approximately 35 days at 28 °C and 50% relative humidity (r.h.). Both the larvae and adults produce a large amount of fine material, frass, and dust while feeding. The adults are long lived and can fly to disperse and initiate new grain infestations (Hagstrum and Throne, 1989).

Grain infestation by *R. dominica* before harvest does not appear to be common (Hagstrum, 2001); thus, infestations primarily result from either residual populations inside storage structures (Reed et al., 2003) or immigration from outside sources. *Rhyzopertha dominica* has been shown to enter grain bins through the eaves, vents, and poorly sealed bin bottoms, and to enter grain storage warehouses through the gaps around overhead doors (Hagstrum, 2001; Toews et al., 2006). The insect is detected in stored grain very soon after grain is brought in for storage (Hagstrum and Throne, 1989; Dowdy and McCaughey, 1994). However, the sources of beetles immigrating into storage facilities remain unclear. One important source is likely dispersing individuals from other infested grain storage sites, but the importance of non-grain habitats remains to be determined.

There has been considerable research conducted on the outdoor flight activity of *R. dominica*. This species has been

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captured in flight traps outside grain storage structures in the southeastern US, and from Texas to Canada (Leos-Martinez et al., 1986; Fields et al., 1993; Throne and Cline, 1994; Dowdy and McCaughey, 1994, 1998; Edde et al., 2005; Toews et al., 2006). Furthermore, these projects were often conducted in diverse native habitats that were far from grain storages (Fields et al., 1993; Edde et al., 2005; Campbell et al., 2006; Ching'oma, 2006; Toews et al., 2006). Ching'oma (2006) showed that these beetles can disperse at least 1000 m from a common release point, and found that early in the season beetle captures in traps placed within woodlands far from grain storage were often greater than captures in traps near grain storage sites. These patterns of trap captures suggest that populations may be exploiting plants and seeds in the landscape in addition to stored grain for reproduction or as food sources to enable adults to persist during periods when stored grain is not available or during long-range dispersal.

Members of the Bostrichidae are typically wood borers, and some early references reported finding *R. dominica* inhabiting wood (see Potter, 1935). Although a few previous studies have been conducted to investigate the use of alternative host plants by *R. dominica*, proof of sustained use of non-grain hosts is limited. Wright et al. (1990) reported that a number of *R. dominica* F1 progeny developed on acorns, *Celtis laevigata* (Willd) (hackberry), and *Ceanothus cuneatus* (Hook) (buckbrush) fruits, and adults were able to survive on fruits of *Prunus angustifolia* (Marsh) (sandhill plum), *Quercus muehlenbergii* (Engelm.) (chinquapin oak), *Celtis* sp. (hackberry), *C. cuneatus*, and *Juglans nigra* (L.) (black walnut). Recently, Edde and Phillips (2006) also examined the reproductive ability of *R. dominica* on seven types of plants including *Triticum aestivum* (L.) (wheat), *Arachis hypogaea* (L.) (peanuts), *Vigna unguiculata* (L.) (cowpea), *Solanum tuberosum* (L.) (dried potato tubers), and *Quercus* sp. (oak). However, it is unclear how commonly these materials are exploited under field conditions.

The host range and role of native habitats have been much more extensively studied in a closely related member of the Bostrichidae, the larger grain borer, *Prostephanus truncatus* (Horn) (Helbig et al., 1992; Nang'ayo et al., 1993; Ramirez-Martinez et al., 1994; Hill et al., 2002; Nansen et al., 2002, 2004). *Prostephanus truncatus* was able to breed on a variety of species of trees from at least seven families in tropical regions, including the families Fabaceae (e.g., *Delonix regia* (Bojer ex Hook)), Moraceae (e.g., *Ficus exasperata* (L.)), Euphorbiaceae (e.g., *Manihot esculenta* (Crantz)), Bombacaceae (e.g., *Ceiba pentandra* (L.)), Anacardiaceae (e.g., *Lannea nigritana* (Scott-Elliott)), and Burseraceae (e.g., *Bursera fagaroides* (Kunth)). In addition, *P. truncatus* was also able to reproduce on the seeds of teak, *Tectona grandis* (L.) (Nansen et al., 2004). Some of these tree species were considered host plants for *P. truncatus* and helped sustain populations (Borgemeister et al., 1998; Nansen et al., 2004), which exploited newly stored grain in Africa.

At multiple locations in Kansas, seasonal patterns in trap captures of *R. dominica* both near and far from grain storage sites have been observed (Ching'oma, 2006; Campbell et al., 2006; Toews et al., 2006). Typically, a large spike in flight activity denoted by pheromone trap catches is observed early in the spring (April), prior to grain harvest and when most farm storage bins have been emptied. The April flight activity is then followed by relatively smaller oscillations in trap catches during the spring and summer followed by some late season flight peaks in late October or early November. In an agricultural landscape, captures often occurred away from grain storage sites, and analysis of the relationships between habitat and trap captures indicates beetle captures are more associated with woodland than grain storage sites (Campbell et al., 2006; Ching'oma, 2006). In a native prairie

habitat (Konza Prairie Biological Research Station, 39.09N, 96.60W, a 3,487-ha native tall-grass prairie preserve that contains grasslands and wooded areas), we have previously observed a similar seasonal pattern in trap capture even though there is only limited grain production and storage within a 15-km radius around the preserve.

The fact that insects are captured well before grain harvest and storage combined with the fact that captures take place many kilometers from grain storage sites suggests that adults may be exploiting non-grain habitats: either surviving on other foods until grain is harvested and stored or populations are reproducing and cycling on these alternative food resources. To evaluate the potential for adult *R. dominica* to survive on resources found in these habitats, we measured adult survival on a range of grass seeds, forb seeds, and tree seeds and wood of species that are typically found in Kansas landscapes where adults are captured.

2. Materials and methods

2.1. Survival of *R. dominica* adults on grass, forb, and shrub seeds

Seeds of 19 dominant and subdominant species of grasses, forbs, and shrubs in Kansas prairie habitats were tested for their ability to support adult *R. dominica* survival. Fourteen species of grasses, four species of forbs, and one shrub species were tested (Table 1). The seed materials were obtained from Lawyer Nursery, Plains, MT, and Prairie Moon Nursery, Winona, MN. The moisture content of the seeds was unknown and they were held at 5 °C after receiving until testing. Twenty recently emerged (one- to two-week-old) adults were taken from a stock colony, which was founded with individuals collected in the field during May 2006 and maintained on *T. aestivum* kernels (13% moisture content) at 28 °C, 50% r.h., and 15L:9D photoperiod. These beetles were introduced along with 2 g of seeds into a 3 cm × 10 cm glass vial with a screen lid. Vials with no seeds served as negative controls and vials with 2 g of *T. aestivum* kernels served as positive controls. Based on preliminary observations of *R. dominica* survival in the absence of food, mortality was assessed after being held for a period of two weeks in a growth chamber at the same environmental conditions under which the beetles were cultured. A two-week observation period was selected based on preliminary data, indicating that this species does not survive past this length of time in the absence of food. If adult survival was observed, then we evaluated the ability of the species to develop from egg to adult on these materials. Two blocks of tests were each performed at different times with typically four replicates per block, although in some cases sufficient seed material could not be procured for the eight replicates (see Table 1).

To assess if increased survival was simply related to additional moisture from the seed material rather than nutritional benefits, survival of *R. dominica* in vials with moist cotton was assessed as described above. A cotton dental wick, 1 × 3 cm, was moistened with water and then placed inside the vials. There were three replicates of this treatment.

2.2. Survival of adult *R. dominica* on tree twigs

Survival of *R. dominica* was also investigated on freshly cut and dead twigs of 22 tree species that occur in Kansas landscapes (see Table 2). Both twigs with fresh leaves (live twigs) and dead branches were cut from the same tree in all cases and used in experiments on the day they were collected. Twigs were cut into 6-cm long lengths for use in experiments (diameter ranging from 7 to 9 mm). Twigs were placed individually into 3 × 10-cm glass

Table 1
Survival of *Rhyzopertha dominica* on seeds of different grass, forb, and shrub species

Plant	Family	Species	Common name	n	Survival (%) (mean ± SEM)		
Grasses	Poaceae	<i>Andropogon gerardii</i> (Vitman)	Big bluestem	8	0.0 ± 0.0 c		
		<i>Elymus canadensis</i> (L.)	Canada wildrye	8	13.4 ± 5.3 b		
		<i>Elymus virginicus</i> (L.)	Virginia wildrye	8	0.0 ± 0.0 c		
		<i>Hordeum jubatum</i> (L.)	Squirrel-tail grass	8	3.2 ± 2.5 c		
		<i>Sorghastrum nutans</i> (Nash)	Indian grass	8	0.6 ± 0.8 c		
		<i>Poa pratensis</i> (L.)	Kentucky bluegrass	8	0.0 ± 0.0 c		
		<i>Leersia oryzoides</i> (L.)	Rice cut grass	8	0.0 ± 0.0 c		
		<i>Schizachyrium scoparium</i> (Nash)	Little bluestem	8	0.0 ± 0.0 c		
		<i>Muhlenbergia racemosa</i> (Michx)	Upland wild timothy	8	0.0 ± 0.0 c		
		<i>Panicum virgatum</i> (L.)	Switch grass	8	0.0 ± 0.0 c		
		<i>Bromus inermis</i> (Leyss)	Smooth brome	8	2.1 ± 2.6 c		
		<i>Sporobolus asper</i> (Michx)	Rough dropseed	8	0.0 ± 0.0 c		
		<i>Tridens flavus</i> (L.)	Purpletop	8	0.6 ± 0.8 c		
		<i>Avena fatua</i> (L.)	Wild oat	3	1.7 ± 1.7 c		
		<i>Triticum aestivum</i> (L.)	Wheat	6	80.3 ± 10.0 a		
		Forbs	Fabaceae	<i>Baptisia leucophaea</i> (Nutt)	Cream wild indigo	4	0.6 ± 0.8 c
				<i>Cassia marilandica</i> (L.)	Maryland senna	8	0.0 ± 0.0 c
Fabaceae	<i>Desmodium glutinosum</i> (Muhl)		Pointed-leaved tick trefoil	6	0.8 ± 1.2 c		
Scrophulariaceae	<i>Scrophularia marilandica</i> (L.)		Late figwort	6	0.0 ± 0.0 c		
Shrubs	Rosaceae	<i>Rosa arkansana</i> (Porter)	Prairie wild rose	8	0.0 ± 0.0 c		
Controls			Blank	6	0.0 ± 0.0 c		
			Wet cotton	6	0.0 ± 0.0 c		

Means in the same column followed by different letters are significantly different (least squares means with Bonferroni corrections).

Table 2
Rhyzopertha dominica survival and tunneling activity on fresh cut and dead twigs of different tree species

Family	Species	Common name	Fresh cut twigs			Dead twigs		
			Survival (%) (mean ± SEM)	Fines index (mean ± SEM)	Number of holes (mean ± SEM)	Survival (%) (mean ± SEM)	Fines index (mean ± SEM)	Number of holes (mean ± SEM)
Aceraceae	<i>Acer rubrum</i> (L.)	Red maple	6.7 ± 3.3 c	2.0 ± 0.0 b	1.7 ± 0.3 bc	8.3 ± 3.3 b	1.0 ± 0.0 c	0.0 ± 0.0 c
	<i>Acer saccharinum</i> (L.)	Silver maple	1.7 ± 1.7 c	2.0 ± 0.6 b	3.7 ± 0.3 ab	5.0 ± 2.9 b	1.0 ± 0.0 c	1.3 ± 0.8 abc
Annonaceae	<i>Pyrus malus</i> (L.)	Apple	5.1 ± 0.1 c	2.0 ± 0.0 b	1.3 ± 0.3 bc	7.0 ± 4.4 b	2.0 ± 0.0 abc	0.0 ± 0.0 c
Cannabaceae	<i>Celtis spp.</i>	Hackberry	5.1 ± 0.1 c	2.0 ± 0.0 b	3.0 ± 0.3 ab	8.3 ± 3.3 b	3.0 ± 0.0 a	0.0 ± 0.0 c
Cupressaceae	<i>Juniperus virginiana</i> (L.)	Eastern red cedar	0.0 ± 0.0 c	1.0 ± 0.0 c	0.3 ± 0.3 c	6.7 ± 3.3 b	1.0 ± 0.0 c	0.0 ± 0.0 c
Dipsacaceae	<i>Dipsacus laciniatus</i> (L.)	Russian olive	1.7 ± 1.7 c	1.0 ± 0.0 c	1.0 ± 0.3 bc	1.8 ± 1.8 b	1.0 ± 0.0 c	0.3 ± 0.3 c
Fagaceae	<i>Quercus macrocarpa</i> (Michx)	Burr oak	8.3 ± 4.4 bc	2.0 ± 0.0 b	1.7 ± 0.3 bc	1.7 ± 1.7 b	1.0 ± 0.0 c	0.0 ± 0.0 c
	<i>Quercus muehlenbergii</i> (Engelm)	Chinquapin oak	6.8 ± 1.8 bc	1.0 ± 0.0 c	0.7 ± 0.3 bc	6.7 ± 1.6 b	1.0 ± 0.0 c	0.3 ± 0.3 c
	<i>Quercus palustris</i> (Muenchh)	Pin oak	11.7 ± 1.7 bc	2.0 ± 0.0 b	1.0 ± 0.3 bc	8.4 ± 3.3 b	1.7 ± 0.3 bc	2.0 ± 0.6 a
	<i>Quercus rubra</i> (L.)	Red oak	6.7 ± 1.7 bc	2.0 ± 0.0 b	2.3 ± 0.3 bc	5.0 ± 2.9 b	1.0 ± 0.0 c	0.7 ± 0.3 abc
Hamamelidaceae	<i>Liquidambar styraciflua</i> (L.)	Sweetgum	6.7 ± 4.4 c	2.0 ± 0.0 b	1.3 ± 0.3 bc	5.2 ± 0.1 b	1.0 ± 0.0 c	1.0 ± 0.6 abc
Juglandaceae	<i>Juglans nigra</i> (L.)	Black walnut	5.0 ± 2.9 c	1.0 ± 0.0 c	0.7 ± 0.3 bc	7.2 ± 3.6 b	2.3 ± 0.7 ab	0.3 ± 0.3 c
	<i>Carya ovata</i> (Mill)	Hickory	8.3 ± 3.3 c	1.7 ± 0.3 b	1.3 ± 0.3 bc	1.8 ± 1.8 b	1.7 ± 0.3 bc	1.3 ± 0.3 abc
Leguminosae	<i>Gleditsia triacanthos</i> (L.)	Honey locust	36.7 ± 10.1 b	3.0 ± 0.0 a	5.0 ± 0.3 a	0.0 ± 0.0 b	1.0 ± 0.0 c	0.0 ± 0.0 c
	<i>Cercis canadensis</i> (L.)	Red bud	5.1 ± 0.1 c	1.0 ± 0.0 c	0.3 ± 0.3 c	8.3 ± 3.3 a	1.3 ± 0.3 bc	1.3 ± 0.3 abc
Moraceae	<i>Morus rubra</i> (L.)	Mulberry	1.6 ± 1.6 c	1.0 ± 0.0 c	0.3 ± 0.3 c	0.0 ± 0.0 b	1.0 ± 0.0 c	0.3 ± 0.3 c
	<i>Maclura pomifera</i> (Raf)	Osage orange	3.3 ± 3.3 c	1.0 ± 0.0 c	2.7 ± 0.3 b	8.3 ± 3.3 b	1.0 ± 0.0 c	0.3 ± 0.3 c
Oleaceae	<i>Fraxinus pennsylvanica</i> (Marsh)	Green ash	6.7 ± 4.4 c	2.0 ± 0.0 b	1.7 ± 0.3 bc	5.0 ± 0.0 b	1.3 ± 0.3 bc	0.7 ± 0.3 abc
Pinaceae	<i>Pinus nigra</i> (Arnold)	Austrian pine	1.7 ± 1.7 c	1.0 ± 0.0 c	0.7 ± 0.7 bc	3.3 ± 1.7 b	2.0 ± 0.0 abc	2.3 ± 0.3 a
Platanaceae	<i>Platanus racemosa</i> (Nutt)	Sycamore	3.3 ± 1.7 c	2.0 ± 0.0 b	3.0 ± 1.5 ab	6.7 ± 1.7 b	1.0 ± 0.0 c	1.0 ± 0.6 abc
Salicaceae	<i>Populus fremontii</i>	Cottonwood	6.7 ± 1.6 bc	2.0 ± 0.0 b	2.7 ± 0.3 b	1.7 ± 1.7 b	1.0 ± 0.0 c	1.0 ± 0.6 abc
Ulmaceae	<i>Ulmus americana</i> (L.)	American elm	3.3 ± 1.7 c	3.0 ± 0.0 a	1.7 ± 0.3 bc	1.7 ± 1.7 b	2.0 ± 0.0 abc	0.7 ± 0.6 abc
Poaceae	<i>Triticum aestivum</i> (L.)	Wheat	100.0 ± 0.0 a			100.0 ± 0.0 a		
Control			0.0 ± 0.0 c			0.0 ± 0.0 b		

Tunneling activity was measured using both an index of the amount of fines (i.e., frass and chewed plant material) produced and the number of entrance holes chewed into wood. Means in the same column followed by different letters are significantly different (least squares means with Bonferroni correction).

vials with screened lids. Twenty recently emerged (1- to 2-week-old) *R. dominica* adults were taken from the stock colony and introduced into each vial. Vials with no twigs served as negative

controls and vials with 2 g of *T. aestivum* kernels served as positive controls. There were two blocks performed at different times with three replicates in each block.

Following a period of two weeks in a growth chamber maintained at 28 °C and 15L:9D photoperiod, *R. dominica* survival was determined. Twigs were dissected to determine survival of any beetles that had tunneled into the twigs. In addition to survival, feeding damage was quantified based on both the number of tunnels and the amount of fines (mixture of frass and powdery plant material resulting from beetle tunneling activity) produced during the two-week period. The number of tunnels bored by *R. dominica* in each twig was measured by counting the number of holes in the outer surface of the twigs. The following index was used to quantify the amount of fines produced: 1—fines absent or only barely visible on the bottom of the vial; 2—fines covered approximately 50% of the bottom of the vial; 3—fines covered the bottom of the vial.

2.3. Survival and reproduction of adult *R. dominica* on tree seeds

Seeds were collected during late October 2006 from 14 tree species common in Kansas landscapes, including five species of oaks (Table 3). Tree seeds were cut in half and 3–4 g were added to each vial. Twenty recently emerged (1- to 2-week-old) *R. dominica* adults were taken from a stock colony that was maintained under the conditions described above. These beetles were added to a glass vial. Vials with no seeds served as blank controls and vials with 2 g of *T. aestivum* kernels served as positive controls. Following a period of two weeks in a growth chamber at 28 °C and 15L:9D photoperiod, survival of *R. dominica* was examined. There were three replicates for each treatment.

This experiment was repeated at a later date, but the protocol was modified to examine longer-term survival and reproduction on tree seeds in glass jars (8 cm × 13 cm). In the follow-up assessment, each jar contained approximately 20 g of seeds. Following a period of four weeks in a growth chamber at 28 °C and 15L:9D photoperiod, survival of *R. dominica* was assessed. In addition, progeny development of *R. dominica* in these seeds was examined by X-raying seeds (Model MX-20, Faxitron X-ray Corporation, Wheeling, IL, USA) and visual examination of radiographs for immatures. After assessment, all dead and living *R. dominica* adults were sieved out of the media and the jars were held under the same environmental conditions for an additional four weeks. At the end of this time period, the seeds in each vial

were manually dissected and the number of adult progeny was counted.

2.4. Influence of tree seed damage on *R. dominica* survival

To assess the natural level of damage to acorns found in the field, over 600 acorns of *Q. muehlenbergii* were collected on the ground at the Konza Prairie Biological Research Station in late October 2006. Acorns were classified into two major categories: damaged or undamaged. Damaged acorns were further categorized into those damaged by insects (with one to three round holes (≈ 2 mm) in the shell of the acorn), rodents (evidence of chewing on the shell), or other (e.g., one or two splits in the shell of the acorn). Furthermore, all of these acorns were held inside sealed jars in the laboratory and regularly sieved to assess emerging insect species.

To assess the influence of acorn damage on potential *R. dominica* exploitation, survival of *R. dominica* on damaged versus undamaged acorns of *Q. rubra* was examined. Treatments included undamaged acorns, acorns previously infested by insects (two small exit holes on the acorn), acorns chewed partially by squirrels or other rodents, and acorns cut in half manually. Each vial contained a single acorn (either damaged or undamaged) and vials with no tree seeds served as negative controls while vials with 2 g of *T. aestivum* kernels served as positive controls. Twenty *R. dominica* adults (1- to 2-week-old) were introduced into each vial and survival of *R. dominica* was recorded at the end of a 2-week period. Experimental conditions were 28 °C and 15L:9D photoperiod. There were three replicates for each treatment. Survival of *R. dominica* was also examined on the undamaged tree seeds of *Cercis canadensis*, *J. nigra*, and *Prunus americana*.

2.5. Statistical analysis

Survivorship, reproduction, frass production, and number of tunnels were analyzed using analysis of variance (mixed model procedure) and multiple comparisons made using least squares means (for unbalanced data, at $P=0.05$) with Bonferroni corrections (SAS 9.1 software, SAS Institute Inc. Cary, NC, USA). Percentage data were arcsine square root transformed prior to analysis, but untransformed data are presented in the results.

Table 3

Rhyzopertha dominica survival and number of F1 progeny produced on seeds of different tree species

Family	Species	Tree (seeds)	Survival (%) (mean \pm SEM) at 2 weeks	Survival (%) (mean \pm SEM) at 4 weeks	F1 adult (mean \pm SEM) by day 67
Cupressaceae	<i>Juniperus virginiana</i> (L.)	Eastern red cedar	1.7 \pm 1.7 c	2.1 \pm 2.1 c	0.0 \pm 0.0 c
Fagaceae	<i>Quercus macrocarpa</i> (Michx)	Burr oak	98.3 \pm 1.7 a	80.1 \pm 5.3 a	9.3 \pm 2.2 b
	<i>Quercus muehlenbergii</i> (Engelm)	Chinquapin oak	100.0 \pm 0.0 a	95.8 \pm 4.2 a	92.3 \pm 9.4 a
	<i>Quercus robur</i> (L.)	English oak	85.2 \pm 9.8 ab	85.3 \pm 2.8 a	12.0 \pm 4.7 b
	<i>Quercus rubra</i> (L.) ^a	Northern red oak	93.3 \pm 1.7 ab	58.0 \pm 12.5 ab	0.3 \pm 0.3 c
	<i>Quercus rubra</i> (L.) ^a	Northern red oak	100.0 \pm 0.0 a	79.8 \pm 6.2 a	0.0 \pm 0.0 c
	<i>Quercus palustris</i> (Muenchh)	Pin oak	100.0 \pm 0.0 a	76.9 \pm 1.1 a	0.3 \pm 0.3 c
	<i>Quercus shumardii</i> (Buckl)	Shumard oak	100.0 \pm 0.0 a	8.8 \pm 3.6 c	0.0 \pm 0.0 c
Hamamelidaceae	<i>Liquidambar styraciflua</i> (L.)	Sweet gum	0.0 \pm 0.0 c	0.0 \pm 0.0 c	0.0 \pm 0.0 c
Juglandaceae	<i>Juglans nigra</i> (L.)	Black walnut	48.9 \pm 26.0 bc	28.8 \pm 3.6 bc	0.0 \pm 0.0 c
Leguminosae	<i>Gleditsia triacanthos</i> (L.)	Honey locust	12.4 \pm 6.5 c	1.6 \pm 0.8 c	0.0 \pm 0.0 c
Moraceae	<i>Maclura pomifera</i> (Raf)	Hedge apple	1.7 \pm 1.7 c	0.7 \pm 0.7 c	0.0 \pm 0.0 c
Oleaceae	<i>Fraxinus Pennsylvania</i> (Marsh)	Sweet ash	11.1 \pm 5.6 c	1.3 \pm 1.3 c	0.3 \pm 0.3 c
Platanaceae	<i>Platanus racemosa</i> (Nutt)	Sycamore	22.0 \pm 11.7 c	0.0 \pm 0.0 c	0.0 \pm 0.0 c
Rosaceae	<i>Pyrus spp.</i>	Crab apple	57.4 \pm 15.2 b	43.8 \pm 13.2 b	0.0 \pm 0.0 c
Poaceae	<i>Triticum aestivum</i> (L.)	Wheat	98.3 \pm 1.7 a	91.9 \pm 1.1 a	113.0 \pm 45.0 a
Control			0.0 \pm 0.0 c		

Means in the same column followed by different letters are significantly different (least squares means with Bonferroni corrections).

^a Collected from two different locations and tested separately.

To avoid violating normality assumptions behind ANOVA, we used the criterion that whenever more than half of the treatments had an average of 100% mortality of beetles (e.g., grass/forbs seeds), treatments with no survivors were excluded from the analysis.

3. Results

3.1. Survival of adult *R. dominica* on grass, forb, and shrub seeds

Rhyzopertha dominica adult survival on the tested seeds, representing 4 families and 18 genera, after two weeks was generally low, and in all but two cases was not significantly greater than in the negative control (ANOVA: $F_{(20, 133)} = 44.9$; $P < 0.001$) (Table 1). Survival over the two-week period was greater than in the negative control only on *T. aestivum* ($80.3 \pm 10.0\%$ survival) and on *Elymus canadensis* ($13.4 \pm 5.3\%$ survival). Interestingly, there was no survival on *E. virginicus*, even though it is in the same genus (Table 1). Seed size was slightly different between *E. canadensis* (5.69 g per 1000 seeds) and *E. virginicus* (7.04 g per 1000 seeds). No observable amount of fines (ground material) was detected in the vials in any of the non-*T. aestivum* treatments.

3.2. Survival of adult *R. dominica* on tree twigs

Survival of *R. dominica* on twigs varied considerably among tree species, ranging from 0% to 36.7% on freshly cut twigs and 0% to 8.4% on dead twigs by the end of the 2-week period (Table 2). Unlike the seed tests, there was a low level of *R. dominica* survival after two weeks in most of the treatments. Of 22 fresh twig tree species tested, *Gleditsia triacanthos* was the only one that supported *R. dominica* survival significantly better than the negative control (ANOVA: $F_{(23, 71)} = 18.3$; $P < 0.001$), and none had survival equivalent to the *T. aestivum* control. A small proportion of adults were also able to survive over two weeks on freshly cut twigs from several other tree species, including the oak species *Q. muehlenbergii*, *Q. macrocarpa*, *Q. palustris*, and *Q. rubra*, although statistically the survival was not significantly different from the negative control, which had no survival after two weeks (Table 2). Due to the high survival of *R. dominica* on *G. triacanthos*, observations of beetles on this species were extended two more weeks and three individuals out of the original 60 were still alive by the end of week 4. There was no significant difference in survival of beetles on freshly cut versus dead twigs of the other species (ANOVA: $F_{(1, 130)} = 0.9$; $P = 0.346$), but there was a significant interaction between tree species and fresh or dead twig (ANOVA: $F_{(21, 88)} = 2.9$; $P < 0.001$). On dead twigs, while there was some survival on all species except *G. triacanthos* and *M. rubra*, none of the tree species supported survival statistically greater than the negative control and only *T. aestivum* had high *R. dominica* survival (ANOVA: $F_{(23, 71)} = 20.2$; $P < 0.001$).

The number of tunnels made by *R. dominica* in twigs during the two-week period ranged from 0 to 5, and varied significantly with tree species (ANOVA: $F_{(21, 44)} = 4.7$; $P < 0.001$ on freshly cut twigs; $F_{(21, 44)} = 2.9$; $P = 0.001$ on dead twigs) (Table 2). The beetles were more likely to tunnel into freshly cut twigs than dead twigs (ANOVA: $F_{(1, 130)} = 25.9$; $P < 0.001$). Because of the performance of this beetle on freshly cut *G. triacanthos* twigs, we measured the depth of the tunnels. The beetles were able to tunnel up to 2.5 cm from the cut edge over the period of two weeks. All tunneling occurred from the cut ends of the wood, with no tunneling observed entering through the bark for any of the tree species. Beetles produced considerably more fines on *Ulmus americana* and *G. triacanthos* freshly cut twigs than on any other tree species

tested, even though survival differed between the two species. Overall, *R. dominica* produced relatively more frass on freshly cut twigs than on dead twigs (ANOVA: $F_{(1, 130)} = 9.0$; $P = 0.003$). One exception was that *R. dominica* produced more fines on dead *Pinus nigra* than on the freshly cut, perhaps due to decreased sap production in the dead twig.

3.3. Survival and reproduction of *R. dominica* on tree seeds

Survival of *R. dominica* on broken tree seeds varied considerably with tree species, ranging from 1.7% to 100% survival after two weeks (Table 3). *Quercus muehlenbergii*, *Q. palustris*, *Q. rubra*, and *Q. shumardii* were the best at sustaining *R. dominica* survival, followed by other oak species, including *Q. macrocarpa* and *Q. robur*. The beetles also survived well on crab apple (*Pyrus* spp.) (Table 3), achieving an average of 57.4% survival during a 2-week period. In a separate 4-week experiment, *R. dominica* survival varied significantly with tree species, ranging from 0% to 95.8%. Again, *Q. muehlenbergii* had the greatest level of *R. dominica* survival, followed by other oak species, but not including *Q. shumardii* (Table 3). *Rhyzopertha dominica* still achieved 43.8% survival on crab apple (*Pyrus* spp.) over the four-week period.

Second and third instar progeny were observed in acorns of three oak species, *Q. muehlenbergii*, *Q. macrocarpa*, and *Q. robur* based on X-ray analyses. Subsequent emergence of F1 adults from acorns was observed and the adults were sieved out and counted on day 67. Significantly more *R. dominica* adults emerged from *Q. muehlenbergii* than from either *Q. macrocarpa* or *Q. robur*. Beetle survival and reproduction on *Q. muehlenbergii* was similar to that on *T. aestivum* kernels (Table 3).

3.4. Influence of tree seed damage on *R. dominica* survival

Approximately 75% of field collected *Q. muehlenbergii* acorns were damaged. Damage primarily was in the form of small, emergence holes caused by members of the Curculionidae; but an additional 10% were damaged by rodents, probably squirrels, or appeared to be simply cracked open mechanically. Three adult *R. dominica* emerged from these 600 field collected acorns, indicating natural infestation of these seeds in the field. In addition, many weevil larvae (*Curculio* spp.) and adult fungus beetles (*Cryptophagus* spp.) were sifted out of the acorns.

The beetles survived equally well on acorns damaged by any method, but could not survive on undamaged acorns (Table 4). Additionally, there was no significant amount of fines on undamaged acorns. Survival of *R. dominica* was also nonexistent on the remaining undamaged tree seeds with hard shells.

4. Discussion

Undamaged seeds of grass, forb, and shrub species found in Kansas landscapes do not appear to support survival of *R. dominica* in natural habitats. Adult *R. dominica* feed readily on twigs of many tree species, which increased short-term survival modestly, but wood did not support high levels of survival or reproduction, suggesting that it is not a good source of nutrition. In contrast, acorns appear to be excellent resources for *R. dominica*, but only if they are already damaged to allow easy entry for the beetles. Acorn shells are naturally broken with seasonal freezing and thawing cycles and shells are commonly damaged by other seed predators so damaged seeds are abundant. The lack of survival on most of the grass and forb seeds and on unbroken tree seeds suggests that *R. dominica* is unable to penetrate the seed coat of many of the seeds present in the environment that would

Table 4
Rhyzopertha dominica survival on damaged vs. undamaged red oak acorns

Family	Species	Tree (Acorn)	Damaged	Survival (%) (mean ± SEM)
Fagaceae	<i>Quercus rubra</i> (L.)	Red oak	Insect exit holes	98.3 ± 1.8 a
			Rodent feeding	96.3 ± 6.4 a
			Halved manually	93.3 ± 1.7 a
			Undamaged (whole)	0.0 ± 0.0 b
Poaceae	<i>Triticum aestivum</i> (L.)	Wheat control	Kernels	98.3 ± 2.9 a
		Blank control		0.0 ± 0.0 b

Means within columns followed by different letters are significantly different (least squares means with Bonferroni corrections).

otherwise be potentially available for exploitation. These findings will help us explore the causes of patterns in spatial and temporal distribution and evaluate the role of alternative foods in *R. dominica* population dynamics in agricultural landscapes.

Rhyzopertha dominica has been reported to develop in woody hosts (Potter, 1935; Highland, 1984), and a closely related species, *P. truncatus*, can successfully exploit woody plant species (Hill et al., 2002; Nansen et al., 2004). In the current study, although *R. dominica* tunneled in many of the woody plants, survival was generally poor. Survival of *R. dominica* on honey locust twigs was significantly higher than the no-food control, and some adults survived up to four weeks. However, survival was still only about 40% compared with 100% on *T. aestivum*. It is possible that *R. dominica* exhibits an ancestral trait of tunneling into wood, but that either the ability to exploit these resources has been lost or that the species tested are not suitable but that other species may still support survival and reproduction. There was also no relationship between the amount of tunneling and how well the beetles survived on these different species of wood. These findings suggest that certain tree species in natural habitats could potentially serve as temporary 'refuges' and sustain *R. dominica* for short periods if there was no other food available, thus helping to facilitate long-range dispersal. Our experiments were no-choice bioassays and because all tunneling began at the cut ends, the relevance of these results to the field situation must be considered carefully. Further studies are necessary to determine if the ends were simply the easiest route or if beetles do not tunnel through bark. It may be that given the proposed origin of *R. dominica* on the Indian subcontinent, the tree species available in Kansas do not provide a suitable resource. If tree species from their original habitat were tested they might be better hosts. For example, *G. triacanthos*, on which we had the highest survival, is a member of a genus that while not diverse in North America has many close relatives in Eastern Asia (Schnabel et al., 2003). It would be interesting to further explore the ability of *R. dominica* to exploit other species in this genus and other species typically found in the subtropical regions of its origin. Finally, although originally collected in pheromone traps placed in a natural habitat area, the *R. dominica* used in this study had been maintained on *T. aestivum* and thus may have lost the ability to exploit these alternative foods.

Prostephanus truncatus is able to not only survive, but also breed on vegetative tissues of a variety of tree species in the tropical regions (Helbig et al., 1992; Nang'ayo et al., 1993; Ramirez-Martinez et al., 1994; Hill et al., 2002; Nansen et al., 2002, 2004). Nansen et al. (2004) examined performance of *P. truncatus* on a variety of tree species native to Africa, and found that fresh branches from 11 tree species and fresh roots from four tree species were attacked heavily by this beetle. Moreover, they also found that this beetle reproduced well on the branches from four species of trees (*Delonix regia*, *Ceiba pentandra*, *Manihot esculenta*, and *Ficus exasperata*) and on the roots from two species

(*F. exasperata* and *Ficus capensis*). Borgemeister et al. (1998) found a number of *P. truncatus* in dissected branches of *L. nigriflora* in southern Benin. The beetle was able to breed on tree species from seven families, suggesting that *P. truncatus* may have a broad range of host plants. Species of trees on which *P. truncatus* can reproduce may be its natural host plants and serve as 'reservoirs,' and other species in forests likely serve as 'refuges' sustaining *P. truncatus* populations in the field (Hill et al., 2002). It would be interesting to explore the ability of *R. dominica* to exploit similar tree species associated with tropical and subtropical areas.

Rhyzopertha dominica survived and reproduced on a variety of tree seeds found in Kansas landscapes. Earlier studies have shown this species to reproduce on acorns of *Q. muehlenbergii* (Wright et al., 1990) and *Q. stellata* (Edde and Phillips, 2006). In addition to these two oak species, *Q. macrocarpa* and *Q. robur* also support the reproduction of *R. dominica*. We also recovered *R. dominica* from field collected acorns; this is the strongest evidence yet that these resources are being exploited in the field. In addition to *Q. muehlenbergii*, Wright et al. (1990) found that *R. dominica* could breed on *C. occidentalis* and *C. cuneatus* fruits. The current study has demonstrated that *R. dominica* can survive on *J. nigra* and *Pyrus* spp.

Rhyzopertha dominica survived and reproduced as well on acorns of *Q. muehlenbergii* as on *T. aestivum* kernels. *Quercus muehlenbergii* is distributed widely along the rivers in Kansas landscapes. Since a majority of *Q. muehlenbergii* acorns collected on the ground in the field were damaged, the lack of ability to penetrate undamaged acorns may not be a practical limiting factor. Although not confirmed here, we suspect acorns from other oak species may have similar levels of damage in the field. Oaks such as *Q. muehlenbergii* and *Q. macrocarpa* are common tree species in Kansas where *R. dominica* were captured (Campbell et al., 2006; Ching'oma, 2006; Toews et al., 2006). Oaks are also common in Oklahoma sites where *R. dominica* is also captured in wooded areas (Edde and Phillips, 2006).

Oaks in the genus *Quercus* include several hundred species, including both deciduous and evergreen species. The genus is native to the northern hemisphere, but is distributed from northern latitudes into tropical regions, including many species found in Asia, the proposed place of origin for *R. dominica*. Most of the oaks we tested are native to North America, including the red oaks (Section Lobatae) (*Q. rubra*, *Q. palustris*, and *Q. shumardii*). However, white oaks (Section *Quercus*) have more of a worldwide distribution and are found in Asia. We tested the white oak species *Q. macrocarpa*, *Q. muehlenbergii*, and *Q. robur*. The first two are native to the Americas, but *Q. robur* was introduced from Europe and Western Asia (Chatonnet and Dubourdieu, 1998). The beetle survived well on all species of oak tested, but reproduction was greatest on the white oak species. Red oaks have higher tannin levels than white oak acorns, and the former are often the preferred acorns of vertebrates (Smallwood et al., 2001). These patterns suggest that oaks could have been exploited by

R. dominica in its place of origin and currently are available for exploitation in wooded areas in Kansas. The pattern of plant utilization, particularly of the different species of oaks, is an interesting question in need of further research.

Natural habitats in Kansas landscapes consist of open prairie and woodlands that have many potential provisions for *R. dominica* to feed on and reproduce in. The patterns of exploitation of the tested plant seeds and twigs support the patterns of trap capture observed where peaks of flight activity occur in the spring and fall in wooded, riparian areas. These are the environments where oak species such as *Q. muehlenbergii* and *Q. macrocarpa* thrive. Although, *R. dominica* is captured in open prairie locations, we did not find that they could exploit the seeds available in these areas and are unlikely to exploit those that might be blown into wooded areas. Wooded natural habitats containing oak tree species such as *Q. muehlenbergii* and *Q. macrocarpa*, may function as a reservoir for *R. dominica* and have an impact on the broader landscape dynamics of flight activity and movement into and out of grain; it is an area in need of further study.

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