OVERWINTERING BEHAVIOUR OF THE NATIVE ELM BARK BEETLE, HYLURGOPINUS RUFIPES (EICHHOFF) (COLEOPTERA: SCOLYTIDAE),

IN MANITOBA

A Thesis Submitted to the Faculty

of

Graduate Studies The University of Manitoba

by

Patricia L. Anderson

In Partial Fulfilment of the

Requirements for the Degree

of

Master of Science Department of Entomology © July 1996

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HYLURGOPINUS RUFIPES (EICHHOFF) (COLEOPTERA: SCOLYTIDAE),

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PATRICIA L. ANDERSON

A Thesis/Practicum submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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my husband, Rob,

who encouraged me to continue when I wanted to give up.

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iv

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TABLE OF CONTENTS

							PAGE
ACKNOWLEDGMENTS	•••	•	•••	•	•	•	iv
TABLE OF CONTENTS	•••	•	• •	•	•	•	v
LIST OF TABLES	•••	•	•••	٠	•	•	viii
LIST OF FIGURES	•••	•	•••	•	•	•	x
LIST OF APPENDICES	•••	•	•••	•	•	•	xiii
ABSTRACT	•••	•	••	•	•	•	xiv
INTRODUCTION		•	••	•	•	•	1
LITERATURE REVIEW	•••	•		•	•	•	7
The Native Elm Bark Beetle	•••	•	•••	•	•	•	7
Morphology	•••	•	•••	•	•	•	7
Life Cycle		•		•	•	•	9
Spring feeding	••	•		•	•	•	10
Oviposition	•••	•		•	•		11
Larval period		•		•	•	•	13
Fall feeding	••	•		•	•	•	15
Overwintering		•		•	•	•	15
Transmission of Dutch Elm Disease	•	•		•	•	•	20

Vector Management	24		
MATERIALS AND METHODS	33		
Emergence Traps	33		
Comparison of Siberian and American Elms	34		
Hole Counts in American Elms - Fall 1992	34		
Bark Dissections - Spring 1993	36		
Hole Counts and Bark Dissections - Fall 1993	37		
Statistical Methods	38		
RESULTS	47		
Emergence Traps	47		
Comparison of Siberian and American Elms	48		
American Elms	54		
Weekly Accumulation of Holes	54		
Effect of Height Above the Ground	57		
Effect of Aspect	64		
Effect of Tree Location	67		
Effect of Tree Size	69		
Effect of Root Flare	81		
Overwintering Survival	83		
Prediction of Beetles from Accumulated Holes	86		
DISCUSSION			
Emergence Traps	89		
Siberian Elms	90		

vi

American Elms	. 91
Prediction of Overwintering H. rufipes From	
Accumulated Holes	. 97
Comparison with Other Bark Beetle Species	. 97
Implication for Vector Management	. 98
CONCLUSIONS	. 100
REFERENCES	101
APPENDIX	. 109

LIST OF TABLES

Tabl	e	PAGE
1.	Elm (Ulmus) species in Manitoba and their relative	9
	resistance to Dutch elm disease	31
2.	Insecticides potentially effective against	
	Hylurgopinus rufipes	32
3.	Site information for comparison of entrance holes	
	in Siberian and American elms near Winnipeg, MB	39
4.	Site information for American elms in Dauphin and	
	Glenlea, MB	40
5.	Mean (\pm S.E.) tree size and density of accumulated	
-	entrance holes for American and Siberian elms .	49
6.	Mean percentage of accumulated entrance holes for	
	each compass aspect in the ground to 25 cm height	
	range for all sites in Dauphin, MB - Fall 1992 and	1
	1993, and direction to the river for each site	66
7.	Mean $(\pm S.E.)$ accumulated entrance holes per	
	100 cm^2 from ground to 25 cm in planted stands	
	of American elms and their adjacent natural	
	stands in Dauphin, MB	68
8.	Relationship of the density of accumulated entrance	ce
	holes, overwintering H. rufipes, and tunnels from	
	ground to 25 cm to tree size and the interaction	
	between tree size and site on American elm trees	
	in Dauphin and Glenlea, MB	71
9.	Results of the iterative process to fit data to	

viii

	the model Mean Density = A / $(1+b(\rho^{DBH}))$ for
	accumulated entrance holes, overwintering H.
	rufipes, and tunnels on American elm trees in
	natural riverbank sites in Dauphin and Glenlea,
	MB
10.	Relationship between the area of the root flare and
	the density of accumulated entrance holes,
	overwintering H. rufipes, and tunnels on American
	in natural riverbank sites in Dauphin, MB - Fall
	1992, Spring and Fall 1993

ix

LIST OF FIGURES

Figu	re	PAGE
1.	Photo of a sample emergence trap used at the	
	University of Manitoba Glenlea Research Station	
	during the spring 1992	41
2.	Location of research sites of American elms near	
	Dauphin, MB for 1992 and 1993	43
3.	Photo of a sample American elm showing the divisio	on
	into sampling units	45
4.	The relationship between the density of accumulate	∋d
	entrance holes on Siberian and American elms in	
	three sites (S1, S2, S3) in Winnipeg, MB	50
5.	Relationship between the density of accumulated	
	entrance holes in Siberian elms and their distance	9
	from an American elm for site S1 in Winnipeg,	
	MB	52
6.	Mean $(\pm S.E.)$ weekly accumulation of entrance	
	holes for each height range on natural and planted	1
	American elms trees in Dauphin, MB - Fall 1992; an	nd
	minimum and maximum temperatures in Dauphin for th	le
	same time period	55
7.	Mean proportion (\pm S.E.) of accumulated	
	entrance holes, overwintering <i>H. rufipes</i> , and	
	tunnels observed for each height above the	
	ground in natural American elms in Dauphin, MB	
	pooled over 1992 and 1993	60

х

- 9. The logistic model fitted to the density of overwintering *H. rufipes* for the ground to 25 cm height range in site ST2 - Fall 1993 73
- 11. Relationship between the density of overwintering adult *H. rufipes* and tree size for the height range ground to 25 cm in natural American elms in Dauphin and Glenlea, MB - Spring 1993 and Fall 1993 . . 77
- 12. Relationship between the density of overwintering tunnels and tree size for the height range ground to 25 cm in natural American elms in Dauphin and Glenlea, MB - Spring 1993 and Fall 1993 79
- 14. The relationship between the accumulation of entrance holes in the fall and the numbers of

xi

LIST OF APPENDICES

Apper	ndix	PAGE
1.	Hylurgopinus rufipes collected from emergence	
	traps at Glenlea, MB - Spring 1992	109

xiii

ABSTRACT

Anderson, Patricia L. M.Sc. Thesis. The Department of Entomology, University of Manitoba, June 1996. Overwintering behaviour of the native elm bark beetle, Hylurgopinus rufipes (Eichhoff) (Coleoptera: Scolytidae), in Manitoba.

Major Professor: Dr. N.J. Holliday

In Manitoba, insecticidal applications are made to control the overwintering stage of the the Dutch elm disease vector, *Hylurgopinus rufipes* (Eichhoff). Unfortunately, little has been published about the exact location of overwintering *H. rufipes* in Manitoba. Thus the objective of this thesis is to examine the overwintering biology of *H. rufipes* in Manitoba with particular reference to the species, size, and location of the tree in which overwintering occurs, and the particular location of overwintering beetles on the tree.

To accomplish the first part of the objective, three sites near Winnipeg where Siberian and American elms coexisted were selected. Entrance holes were counted at weekly intervals in the bottom 35 cm of the trunks of the trees during the fall of 1992. *Hylurgopinus rufipes* was able to overwinter in Siberian elms, but overwintering in Siberian elms occured only where Siberian elms were relatively close to

xiv

American elm and where there was a high population density of *H. rufipes*.

To accomplish the remaining objectives, six sites of American elm near Dauphin, MB and one site near Glenlea, MB were selected. The sites consisted of four natural riverbank locations and three planted stands. Sampled trees were divided into north south east and west aspects at four sampling heights: 0 to 25 cm , 55 to 80 cm, 110 to 135 cm, and 165 to 190 cm. Entrance holes were counted weekly in fall, 1992 and four times in fall, 1993 to estimate the seasonal accumulations of entrance holes. In spring, 1993 and fall, 1993 sample trees were felled, the sampling units dissected, and the numbers of *H. rufipes* and overwintering tunnels in each sample recorded.

Ninety-five percent of the overwintering *H. rufipes* were found on trees greater than 15 cm DBH. The density of overwintering beetles did not increase with tree size above this size. In spring, no living beetles were found on trees less than 8 cm DBH. The accumulation of entrance holes was significantly greater in natural riverbank American elms than in adjacent planted trees. Ninety-six percent of the overwintering *H. rufipes* were found in the ground to 25 cm height range, whereas only about 50% of the holes and tunnels were found in this height range. It is likely that holes and tunnels above this range were made during feeding activity. Aspect and the area of root flare had no effect on the density

XV

of *H. rufipes* in a sample. Insecticidal applications may be restricted to the bottom 55 cm of American elms greater than 15 cm DBH. When *H. rufipes* are abundant, Siberian elms near American elms should also be treated.

- 300

INTRODUCTION

Dutch elm disease is one of the most important diseases of urban trees in the northern hemisphere. The history of Dutch elm disease is described by Strobel and Lanier (1981) and is summarized here. The disease was first identified affecting elms in the Netherlands by Dutch botanist Diana Spierenburg in 1919 and the causative agent was identified by another Dutch scientist, Marie Beatrice Schwarz, in 1921. Dutch elm disease was first detected in North America in Cleveland, Ohio in 1930, although this focus was said to be eradicated. However, simultaneous disease foci were identified in New York City, New Jersey, and southeastern Connecticut shortly after. It was not until 1934 that William Middleton of the U.S. Department of Agriculture's Bureau of Entomology and Plant Quarantine identified bark beetles as the vectors of Dutch elm disease around the world. The first detection of Dutch elm disease in Canada was in southern In 1975, Dutch elm disease was detected Quebec in 1944. simultaneously in Winnipeg, Selkirk, and Brandon, Manitoba (Hildahl 1977). Presently, Dutch elm disease may be found throughout southern and central Manitoba and into Saskatchewan, wherever wild elms exist (Westwood 1996).

Dutch elm disease is caused by a vascular wilt fungus, Ophiostoma ulmi (Buism.) Nannf. syn. Ceratocystis ulmi (Buism.) Moreau. This fungus interferes with the xylem

vessels' conduction mechanism causing the characteristic symptoms of the disease: leaf yellowing and drop followed by branch dieback and eventual tree mortality (Strobel and Lanier 1981). All elm (Ulmus) species are susceptible to some degree to Dutch elm disease, although some species are affected more than others (Campana and Stipes 1981; Heybroek, 1981). On a world wide basis, the American elm, Ulmus americana L., is the most susceptible elm species known (Campana and Stipes 1981). Elm species found in Manitoba and their relative resistance to Dutch elm disease are summarized in Table 1.

Ophiostoma ulmi exists as three main subgroups; the nonaggressive strain and the Eurasian and North American races of the aggressive strain (Brasier 1988). Recently, however, Braiser (1991) suggested that the aggressive and nonaggressive strains be divided into two species, O. novoulmi and O. ulmi respectively. It is believed that O. ulmi was responsible for the first epidemic of Dutch elm disease in the 1920's and 1930's and that O. novo-ulmi is responsible for the current epidemic across North America, Europe, and southwest Asia (Brasier 1991). More detailed information on the fungus and its relationship to Dutch elm disease may be found in Strobel and Lanier (1981), Brasier (1986; 1988), and Sticklen and Sherald (1993).

There are three main modes of transmission of Dutch elm disease: on unsterilized pruning equipment, through natural root grafts of trees less than 13 m apart, and by elm bark

beetles (Scolytidae) (Strobel and Lanier 1981). Of the three, populations of bark beetles have the most impact on the spread of this disease (Strobel and Lanier 1981). In North America, there are two species of bark beetles which vector Dutch elm disease, the smaller European elm bark beetle, Scolytus multistriatus Marsham, and the native elm bark beetle, Hylurgopinus rufipes (Eichhoff). Hylurgopinus rufipes may be found throughout the natural range of American elm in North America as well as locations outside the natural range where American elm has been planted (Hildahl and Wong 1965; Bright 1976). Where the two species of bark beetles coexist, S. multistriatus out-competes H. rufipes and soon eliminates it from the area (Strobel and Lanier 1981; Lanier 1982). However, the distribution of S. multistriatus is limited by the inability of larvae to tolerate temperatures lower than -20°C (Lanier and Peacock 1981; Strobel and Lanier 1981). Although limited numbers of S. multistriatus have been found in Manitoba (Buth and Ellis 1981; 1982; Westwood 1996), Η. rufipes is the primary vector of Dutch elm disease in Manitoba.

A detailed cost-benefit analysis of the Dutch elm disease management program in Manitoba was completed by Westwood (1991). The estimated value of all urban elm trees in communities with Dutch elm disease management programs in Manitoba exceeded \$1.1 billion. The value of wild elm trees is largely unknown, with the exception of the small amount of

elm used for hardwood lumber (Campana and Stipes 1981). From 1975 to 1990, rural communities in Manitoba lost an average of 2.4% of their elms per year and Winnipeg's average annual loss rate has been 2.6%. The average annual cost of Manitoba's integrated management program in rural communities has been approximately \$1.0 million, representing approximately 0.2% of the value of urban elm trees. Any increase in the annual loss rate would result in a large increase in the direct costs for elm removal, replacement trees, and decreased real estate values. If Dutch elm disease was not managed in Manitoba, it could be expected that at least 80% of the elms would be dead in 5 to 10 years, loss rates that have been experienced by other North American cities (Strobel and Lanier 1981). Fredericton, NB is an example where Dutch elm disease management has been successful. After 30 years, the city has retained approximately 70% of its original elm population, but surrounding unmanaged areas are devoid of elms (Magasi et al. 1993). This control comes at an annual cost of approximately \$340,000 (Magasi et al. 1993).

There are six strategies needed in any integrated control program for Dutch elm disease (Strobel and Lanier 1981): exclusion by quarantine where possible, sanitation of diseased and dead elms, care of healthy elms through pruning, watering and fertilizing, reduction of the rate of reproduction of the fungus and vector, protection of valuable trees with

fungicides and /or insecticides, and replacement of elms with alternate species. Manitoba's unique situation of having only one vector species, H. rufipes, allows vector suppression to play a greater part in the integrated control of Dutch elm disease. In addition, it appears that in Manitoba all or nearly all the beetles overwinter as adults at the base of elm trees (Pines and Pines, personal communication; Ellis, unpublished data). This characteristic allows control of a large proportion of the population with a single insecticide application. Basal spraying has become a key component of the integrated management of Dutch elm disease in Manitoba. The City of Winnipeg sprayed over 85,600 elms in 1994 at a cost of approximately \$110,000 (Nixon, personal communication).

To date, little has been published about the exact location of overwintering adult *H. rufipes* in Manitoba. If it were known exactly where the beetles were overwintering, then insecticides could be targeted more specifically, reducing both cost of control and risk of environmental contamination with insecticides. Thus, the objective of this thesis was to determine the overwintering biology of *H. rufipes* under prairie conditions, with particular reference to tree species, tree size, tree location, and the particular location on a tree.

In previous studies, researchers attempted to estimate the numbers of overwintering beetles on a tree by counting the

dust piles created by the beetles boring into their overwintering tunnels (Anderson and Sloan 1980; Gardiner and Webb 1980; Gardiner 1981; Buth and Ellis 1982; Landwehr et al. 1982; Swedenborg et al. 1988; Magasi et al. 1993). However, dust piles are removed by wind and rain, and so observed numbers of dust piles depend on exposure (*i.e.* height, aspect, and proximity of shelter), and time elapsed since rain or wind. In addition, two beetles boring close together will produce what looks like a single dust pile. Thus, a second objective of my thesis was to determine if the numbers of overwintering beetles in a sample could be accurately estimated by counting holes in the bark.

This thesis is organized in traditional style. It consists of six major parts: Introduction, Literature Review, Materials and Methods, Results, Discussion and Conclusions. The Literature Review contains information on the description and life history of the native elm bark beetle, the role of the native elm bark beetle in the transmission of Dutch elm disease, and methods of managing native elm bark beetle populations. The Materials and Methods, Results, Discussion, and Conclusions deal with the thesis research.

LITERATURE REVIEW

The Native Elm Bark Beetle (Hylurgopinus rufipes)

According to Wood (1982) the native elm bark beetle belongs to the genus *Hylurgopinus* in the tribe Tomicini of the family Scolytidae. It is the only known member of this genus. Within the tribe Tomicini, the genus *Hylurgopinus* is closely allied to the genera *Pseudohylesinus* and *Dendroctonus*.

Morphology

A detailed description of all the life stages of H. rufipes was completed by Kaston (1936) in Connecticut.

Egg galleries of *H. rufipes* are oriented across the grain of the wood (Kaston 1939; Lanier 1978). Eggs are usually laid closely packed together on both sides of the gallery (Kaston 1939). Eggs are shiny and pearly white (Kaston 1936). They are oblong to oval, and measure approximately 0.66 mm by 0.38 mm (Kaston 1936).

Hylurgopinus rufipes larvae are legless, white grubs with amber coloured head capsules (Kaston 1936; Lanier 1978). The body is C-shaped and is capable of contracting and expanding considerably (Kaston 1936). Hylurgopinus rufipes larvae develop through either five or six instars (Kaston 1939). Reasons for the difference in the number of instars are unknown, but may be due to sexual variation, environmental

factors, or genetic variation (Kaston 1939). Except for size, there is little difference between the larval instars (Kaston 1936). Full grown larvae are 3.5 to 4 mm long with a head capsule width of 0.8 to 0.9 mm (Kaston 1936). The width of the head capsule is about 3/4 that of the body, distinguishing it from the larvae of the *S. multistriatus*, where the head capsule is 1/2 the width of the body (Lanier 1978).

The appearance of the pupal stage of *H. rufipes* varies depending on size of the pupal chamber and stage of pupal development. In general the pupa is about 3.3 mm long and about 1.5 mm at the widest point (Kaston 1936). The body is covered by a number of setae, which are as pronounced at the end of the pupal period as at the beginning (Kaston 1936). As the pupa ages, the head region changes gradually from entirely white to brownish red (Kaston 1939). The body remains white until after the adult emerges, although it then quickly darkens (Kaston 1939). Pupae can be sexed by comparing the seventh and eighth abdominal tergites (Kaston 1936). In females, tergite seven is enlarged and only a portion of tergite eight is exposed. In males, tergites seven and eight are equal in length. There are also intersexual differences in the shape and curvature of these tergites.

Hylurgopinus rufipes adults are 2.0 to 3.5 mm long and a uniform grey brown (Kaston 1936; Bright 1976; Lanier 1978). Adults tend to darken as they age, and the head and thorax are usually darker than the rest of the body (Kaston 1936).

The head is hypognathous, with only a small portion visible from above (Kaston 1936). The antennae are clubbed and are about twice as long as wide (Kaston 1936). Male and female H. rufipes differ distinctly in abdominal characteristics. On the seventh tergite, males possess processes that serve as stridulatory plectra, whereas the seventh tergite of females is rounded (Kaston 1936; Lyons 1982). A series of parallel ridges on the underside of the apex of the left elytron, found in both males and females, serves as the stridulatory pars However, in the male the file is significantly stridens. longer and has more ridges than in the female (Lyons 1982). These differences may explain the male's ability to stridulate, while stridulation has not been observed in the female (Lyons 1982). Adult H. rufipes may be easily distinguished from S. multistriatus by the shape of the abdomen; the former has a rounded convex shape and the latter a concave posterior (Lanier 1978).

Life Cycle

The life cycle of *H. rufipes* in Connecticut was described in detail by Kaston (1939). Other descriptions may be found in Martin (1938), Thompson and Matthysse (1972) and Swedenborg et al. (1988). These descriptions vary little in the timing of the various life stages, regardless of the different geographical locations.

Spring feeding. Hibernating adult beetles become active early in the spring and generally tunnel further into their overwintering tunnel before emerging (Kaston 1939; Thompson and Matthysse 1972; Lanier 1978). When air temperatures reach about 20°C, beetles leave their overwintering sites and begin to fly (Lanier 1978). This usually occurs in late April or early May. Adult H. rufipes crawl or fly to the canopy of healthy American elms to feed, often in the same tree as they overwintered (Kaston 1939; Lanier 1978). More beetles are attracted to those trees with pruning wounds than those without wounds or those where the wounds had been treated, and beetles are found in greater numbers within 1 m of untreated wounds (Landwehr et al. 1981; 1982). Beetles bore feeding tunnels in branches of 2 to 10 cm diameter (Thompson and Matthysse 1972; Lanier 1978). The feeding tunnels usually reach the phloem layer and score the wood (Lanier 1978).

Borg and Norris (1969) surmised that the feeding responses of *H. rufipes* and *S. multistriatus* differed as they were not stimulated to feed by the same elm extracts. Also, *H. rufipes* showed decreased feeding on 320 μ m thick pith discs, and increased feeding on 1 mm thick pith discs when compared to *S. multistriatus*. This response is probably related to the physical characteristics of their natural feeding sites in healthy elms: *H. rufipes* feeds primarily in the rough bark of the trunk and larger branches, but *S. multistriatus* feeds predominantly on the smooth bark of 2 to 4 year old twigs

(Borg and Norris 1969).

Oviposition. After feeding in the spring, adult *H. rufipes* locate a suitable host for brood development. Gallery construction and oviposition take place during May and June. *Hylurgopinus rufipes* is a poor disperser and has a preference for forest habitat (Martin 1938; Kaston 1939; Lanier 1978). Logs placed in the shade are colonized to a greater extent than those in the sunshine (Martin 1938; Kaston 1939). *Scolytus multistriatus* readily colonizes elms along streets and in open parks, but *H. rufipes* prefers shaded areas such as woodlots, riverbanks, and shelterbelts (Lanier 1978).

11

Hylurgopinus rufipes locates its host by chemosensory means, and can identify hosts that are suitable for breeding prior to bark penetration (Lanier 1982; 1983; Miller et al. 1986). Hosts suitable for breeding are stressed, moribund or cut elms (Lanier 1982; Miller et al. 1986). Healthy trees are not used for oviposition (Miller et al. 1986). The beetles are most sensitive to odors from moribund elms in the spring, after overwintering (Lanier 1982; 1983). Females responding to host volatiles initiate an entrance gallery. Entrance galleries are cut perpendicular to the wood surface, directly into the wood (Kaston 1939). Males use host volatiles to locate the host and some unknown short range cues to locate the gallery entrance (Swedenborg et al. 1989). At the gallery entrance, males stridulate to communicate their presence and

readiness to mate (Swedenborg et al. 1989). Stridulation of two or more rival males at a gallery opening also occurs, and results in only a single male remaining, often the one that arrived first (Swedenborg et al. 1988; 1989). Females do not stridulate (Lyons 1982; Swedenborg et al. 1988; 1989).

NO one has been able to isolate a pheromone that attracts *H. rufipes* (Lanier 1982; 1983; Miller et al. 1986; Swedenborg et al. 1988). Logs containing males, females, or both sexes are as attractive as uninfested logs to both sexes of adult beetles (Lanier 1982; 1983; Miller et al. 1986; Swedenborg et al. 1988). It appears that beetles are attracted by host odour alone, as extracts of host odour attract beetles in the field (Lanier 1982; Miller et al. 1986). However, diseased elm logs are more attractive to *H. rufipes* than any of the elm volatile extracts (Miller et al. 1986).

Scolytus multistriatus adults are able to colonize Siberian (U. pumila L.), and English (U. procera Salisb.) elms successfully, but the number of offspring per parent pair is reduced when colonization occurs on Chinese (U. parvifolia Jacq.) elm (Svihra and Volney 1983). Whether H. rufipes can also colonize these tree species is unknown. Hildahl and Wong (1965) failed to find H. rufipes on Siberian and Chinese elms. Hylurgopinus rufipes adults of both sexes confined on pin or fire cherry (Prunus pennsylvanica L.), white ash (Fraxinus americana L.), and basswood (Tilia glabra Vent.)(T. amerciana L.) died in the containers rather than construct galleries

(Lanier, 1983). It is likely that reports (Kaston 1939; Baker 1972) of these hosts being attacked by *H. rufipes* are misidentifications of either the beetle or the host.

Egg galleries of *H. rufipes* are formed in the inner bark of the host. They generally have an entrance hole near the centre of the gallery with two tunnels extending across the grain of the wood (Becker 1935; Kaston 1939). Eggs are packed in niches along both sides of the gallery (Becker 1935; Kaston 1939). The average number of eggs produced by a female is about 60 (Martin 1938; Kaston 1939). Incubation is dependent on temperature, but generally eggs hatch after about a week (Kaston 1939).

After constructing an egg gallery, females may reemerge, locate another host, and produce a second egg gallery (Gardiner and Roden 1977; Strobel and Lanier 1981; Swedenborg et al. 1988). It is not known whether they mate again before laying a second batch of eggs.

Larval period. Hylurgopinus rufipes larvae feed along the grain of the wood, perpendicular to the egg gallery (Kaston 1939). Larvae feed along the interface between the bark and the wood, often scoring the wood (Kaston 1939; Lanier 1978). Orientation of larval tunnels is often used as a diagnostic characteristic because *S. multistriatus* larval tunnels run across the grain of the wood (Wood 1982). Hylurgopinus rufipes larval tunnels are generally 50 and 65 mm in length,

although there is a great deal of variation (Kaston 1939). This variation is not related to the duration of the larval stage. Larval development is generally completed by late June or early July in Connecticut, but may extend into August in the northern parts of the beetle's range, or in years with low summer temperatures (Kaston 1939). The larval stage may contribute to the dispersal of *H. rufipes*, as infested elm logs are frequently carried down rivers.

Intraspecific competition plays a significant role in the survival of larval broods. Elm wood dries out very quickly after larval tunnels have been formed, thus making it unsuitable for later larvae. Landwehr et al. (1982) found that the same number of surviving offspring are produced by two, three or five mated females per 100 cm². Where the two species coexist in the same host, faster growing *S. multistriatus* larvae utilize host resources before *H. rufipes* larvae, thus eliminating *H. rufipes* from the population (Lanier 1978).

The last instar larva of *H. rufipes* spends approximately a day constructing a pupal cell in the inner bark (Kaston 1939). During the next two days the pre-pupal larva is quiescent. The pupal stage lasts about one to two weeks, depending on temperature (Kaston 1939). Callow adults cut their way out of the pupal cell after their elytra harden and darken (Kaston 1939). Emergence of new adults occurs over several months, usually peaking in late July and early August.

Adult emergence may be earlier if temperatures have been consistently high, or may be later in colder climates.

Fall feeding. Adult H. rufipes, emerging from pupal chambers in late summer, fly to healthy American elm trees and excavate feeding tunnels. Hylurgopinus rufipes adults flying in the late summer and early fall land on a variety of vertical objects, thus how they locate a suitable host is unknown (Lanier 1982; 1983). It appears that these beetles do not fly long distances, but go to the nearest healthy elm (Becker 1935; Kaston 1939). However, there is some evidence that H. rufipes may fly farther than previously thought (Pines and Westwood, unpublished data). Beetles may be using rivers as corridors for dispersal. Unlike in the spring, trees with pruning wounds are not more attractive to H. rufipes than unpruned trees (Landwehr et al. 1981). Feeding tunnels are similar in shape and size to overwintering tunnels (Becker 1937; Kaston and Riggs 1938). These feeding tunnels may be found in all parts of the tree, but are less dense in the canopy than in the lower trunk and large branches (Becker 1937). Feeding generally continues into September, when the beetles seek overwintering sites (Finnegan 1957; Lanier 1983).

Overwintering. As the temperature drops, *H. rufipes* adults move from the branches to the base of the tree to overwinter (Lanier 1983). Overwintering tunnels are seldom greater than

2 cm long and may extend in any direction in relation to the grain of the wood (Becker 1935; Kaston and Riggs 1938). On occasion, overwintering tunnels may extend into the sapwood (Becker 1935).

Landwehr et al. (1982) in Minnesota, found 97% and 89% of the dust piles created by overwintering *H. rufipes* on a tree were within 30 and 15 cm of the ground, respectively. They confirmed that this distribution is indicative of beetle presence by removing the bark and counting the beetles. Unfortunately, they did not report their counts of beetles. Ellis (unpublished data) found that in Manitoba the majority of dust piles created by overwintering *H. rufipes* are less than 15 cm from the ground. In Massachusetts, the greatest number of overwintering tunnels are near the ground on the trunk and on the exposed roots of elm trees (Becker 1935). Several other authors have observed a greater number of overwintering beetles near the ground; unfortunately, these observations were not quantitative (Thompson and Matthysse 1972; Gardiner and Webb 1980).

Other researchers have found adult *H. rufipes* apparently overwintering higher in the tree (Kaston and Riggs 1938; Kaston 1939; Anderson and Sloan 1980; Gardiner and Webb 1980), although in most cases, densities of overwintering adults or counted dust piles were greatest closer to the ground. Kaston and Riggs (1938) and Kaston (1939) in Connecticut found only 25% of the tunnels in the bark above 80 cm contained beetles

in September however, the proportion of unoccupied tunnels in the same height ranges increased in October and November. These were likely feeding tunnels, as Kaston and Riggs did not look for overwintering beetles closer to the ground, and the numbers of overwintering beetles are much lower than would be expected from the rest of the life history data found in the paper. Anderson and Sloan (1980) found boring dust piles at 1.25 m above the ground in October in Minnesota. It is possible, although unlikely, that these are from feeding tunnels, but without weather information, this cannot be determined. The large number of samples where dust piles were absent would suggest that overwintering was not common at this height.

The presence of snow around the base of the tree has no effect on the success of overwintering *H. rufipes*, even at temperatures as low as -30° C (Landwehr et al. 1982). Survival of overwintering adult beetles decreases with increasing height on the tree (Kaston, 1939), and is attributed to thicker bark in the lower portions of the tree.

New adult *H. rufipes* emerging in late summer may construct egg galleries in dying trees instead of feeding in healthy ones (Becker 1937; Kaston 1939; Finnegan 1957; Thompson and Matthysse 1972; Landwehr et al. 1982; Lanier 1983; Miller et al. 1986). Beetle-infested logs attract more *H. rufipes* than uninfested logs, even though this is not the case in the spring (Miller et al. 1986).

The percentage of the population producing a second generation is usually low (Lanier 1983), but varies greatly geographically. Pines and Pines (personal communication) found that in Manitoba, colonization of moribund elm wood did not occur in August, which is when beetles emerging in the summer would be expected to breed. In addition, they were unable to locate overwintering larvae. When beetles emerging in the summer are confined on host material, less than 4% establish brood galleries (Pines and Pines 1983). Becker (1935; 1939) found overwintering larvae only in some years in Amherst, MA., but did succeed in establishing a colony with beetles collected in the autumn. Gardiner and Roden (1977) in Sault Ste. Marie, ON found adults collected in the fall do not breed without at least 10 weeks at low temperatures, but that this is not an obligate diapause because continuous generations can be produced in the laboratory. In Sault Ste. Marie, ON, H. rufipes are not attracted to moribund elm after mid-August (Gardiner 1979). In Minnesota, summer emerging adult H. rufipes also are not attracted to broodwood (Swedenborg et al. 1988). Landwehr et al. (1982) found second generation brood development in elm wood in July and August in Minnesota in only six of 46 study areas; there appears to be a link between the production of a second generation and both large populations of H. rufipes and availability of suitable broodwood. In the laboratory, however, when summer emerging beetles were confined on

broodwood, only 34% produced egg galleries (Landwehr et al. 1982). Thompson and Matthysse (1972) concluded that *H. rufipes* in New York has one plus a partial second generation per year, with a given cohort overwintering as adults one year and as larvae the next. It appears that there is some environmental cue conditioning beetles to overwinter, possibly photoperiod. The initiation of a second generation has also been observed in southwestern Ontario (Finnegan 1957), in Quebec (Finnegan 1957), Connecticut (Kaston, 1939) and New York (Martin 1938; Thompson and Matthysse 1972), however, the frequency of occurrence in these locations is unknown.

Unlike S. multistriatus larvae, the larvae of H. rufipes can survive freezing temperatures. Kaston (1939) showed overwintering H. rufipes larvae can survive exposure to -28°C, the lowest temperature tested. There is evidence of a true diapause, as none of the larvae that have already begun spring feeding are able to survive freezing (Kaston, 1939). Overwintering larvae begin to develop as temperature permits, complete development, and emerge as adults in June and July (Finnegan 1957; Thompson and Matthysse 1972; Lanier 1978). These adults produce offspring which may either overwinter as larvae or adults depending on the rate of development (Landwehr et al. 1982).
Transmission of Dutch Elm Disease

Although many families of insects and mites occur in diseased elm and may carry *O. ulmi* spores, only bark beetles are proven vectors of Dutch elm disease (Lanier and Peacock 1981). This is because, of all these families, only bark beetles inflict wounds on healthy trees, a process necessary for transmission (Lanier 1978; Lanier and Peacock 1981). Worldwide, there are four species of bark beetles that are the main vectors of Dutch elm disease and an additional sixteen species which are occasional or suspected vectors of the disease (Lanier and Peacock 1981).

The ability of H. rufipes to transmit Dutch elm disease was discovered concurrently by two scientists, Britton (1935) and Collins (1935). In both cases, Dutch elm disease affected American elms in areas where S. multistriatus had not yet become established. Scolytus multistriatus is excluded from areas where temperatures of -20°C occur, due to the vulnerability of the overwintering larvae (Strobel and Lanier 1981; Lanier and Peacock 1981; Lanier et al. 1984). Thus, in the northern parts of the range of American elm, including Canada, H. rufipes is the primary vector of Dutch elm disease (Lyons 1982; Landwehr 1982). et al. s. Although multistriatus occurs in Manitoba (Buth and Ellis 1981; 1982), only isolated specimens have been found, and no breeding population has been identified (Westwood 1996). In Manitoba,

H. rufipes, is the sole vector of Dutch elm disease (Buth and Ellis 1982; Westwood 1996).

Adult elm bark beetles acquire fungal spores when they have pupated in a colonized gallery. The gallery may be inoculated by an infected parent beetle or by formation in wood already infected with Dutch elm disease (Webber and Brasier 1984). The fungus grows through the larval galleries producing spores in the beetle pupal chambers. The number of spores carried by an adult beetle depends on a variety of factors. These include initial abundance of spores, arthropod grazing pressure, microbial antagonism, host tree defence, and location of the pupal chamber (Webber and Brasier 1984). Pupal cells in the outer bark appear to contain less inoculum than those in the inner bark. Sixty to 90 % of newly emerging adults carry fungal spores upon leaving the pupal chamber (Webber and Brasier 1984). This percentage is reduced through spore loss to 10 to 50% of the beetles contaminated arriving at a feeding site in the upper canopy. Although the percentage of feeding grooves contaminated with the fungal spores is about the same as the percentage of beetles carrying them, only 3 to 5% of inoculations results in xylem infection (Webber and Brasier 1984). These percentages are based on studies with S. multistriatus, and may not be applicable to H. rufipes. Takai et al. (1979) found 0 to 74% of feeding attempts by H. rufipes to result in inoculation.

Adult H. rufipes undergo a cycle of feeding,

overwintering, then feeding again after emerging from the pupal cell, which may result in fungal spore loss. Fungal recovery from adult H. rufipes in the spring averages 45% in southern Ontario (Takai et al. 1979). Also, adult H. rufipes feed in the larger branches, where the chance of xylem contact is less, potentially decreasing disease transmission. However, trees are more likely to become infected with Dutch elm disease if inoculation occurs in large branches; when inoculation occurs in smaller twigs trees are sometimes able to isolate the infection (Thompson and Matthysse 1972). Hylurgopinus rufipes pupates almost exclusively in the inner bark (Kaston 1939), which favours increased spore production by the fungus, and more inoculum on emerging beetles (Webber and Brasier 1984). In addition, H. rufipes pupates in July and August, when spore production in the pupal chambers is at a maximum (Webber and Brasier 1984). Adults emerging from broodwood in Quebec in August are more likely to carry Dutch elm disease spores than those emerging earlier or later; in this area, a maximum of 50% of the beetles are infective (Pomerleau 1965a). Gardiner and Roden (1977) found that in Sault Ste. Marie, ON, overwintering adult beetles carry a high fungal spore load, and maintain it over a long period of time, but that adults developing from overwintering larvae carry few fungal spores.

The transmission of Dutch elm disease through feeding damage appears to be seasonally limited. Healthy elm trees

are more susceptible to the Dutch elm disease pathogen while they are producing 'early wood', from late May to early July (Pomerleau 1965b; Thompson and Matthysse 1972; Lanier 1978). Feeding in June and early July results in Dutch elm disease transmission, whereas feeding earlier or later in the season does not (Takai et al. 1979). While xylem contact is made by beetles feeding in the fall before overwintering, it does not usually result in Dutch elm disease transmission (Thompson and Matthysse 1972). The same pattern results from mechanical inoculations, so seasonal resistance appears to be related to tree physiology, not to beetle transmission (Takai et al. In Quebec, mechanical inoculation also produces higher 1979). infection rates from May to July than at other times, although low rates of infection occur throughout the year (Pomerleau 1965b). In the northern range of the elm, the period of elm susceptibility is extended due to the slower rate of growth (Lanier 1978), allowing beetles that overwintered as larvae a role in transmission. However, as one goes north, a smaller percentage of the beetles overwinter as larvae and adults from these larvae carry fewer spores. Thus the overwintering adult native elm bark beetles are the most important vectors in northern regions.

Transmission may also occur as the beetles extend their overwintering tunnels in the spring, although it is rare that these extensions make xylem contact (Thompson and Matthysse 1972; Lanier 1978). Xylem contact during overwintering

generally occurs in trees with diameters between 5 and 25 cm (Lanier 1978). Beetles generally do not survive the winter in trees less than 5 cm, and in trees greater than 25 cm the bark is too thick for overwintering tunnels to result in xylem wounds (Thompson and Matthysse 1972; Lanier 1978).

The non-aggressive strain of the Dutch elm disease fungus reaches an equilibrium with both the host and the vectors (Brasier 1986). Following xylem infection, only a limited amount of branch dieback occurs, which keeps the vector population small and limits transmission. However, the aggressive strains create an explosive epidemic (Brasier 1986). Infections lead to tree death, creating an increasing amount of suitable beetle breeding habitat, leading to massive expansions of beetle and fungal populations, until all mature elms are dead and the populations of beetles and fungus crash.

Vector Management

The primary mechanism for the control of *H. rufipes* is to remove any suitable breeding material, a process called sanitation. Timing of sanitation efforts is critical for successful vector control (Campana and Stipes 1981). In areas where *H. rufipes* has only one generation per year, most trees do not become suitable breeding habitat until the second year after infection with Dutch elm disease (Landwehr et al. 1982), thus allowing time to tag and remove infected trees before

beetle colonization. Wood that has already produced a brood of beetles, or that has been dead for more than one year is no longer suitable breeding habitat (Lanier 1982). Sanitation is a necessary part of any integrated control for Dutch elm disease, and any program without it is destined to fail (Peacock 1975; Campana and Stipes 1981). In areas where *H. rufipes* overwinters as both larvae and adults, sanitation is a necessary back up to any efforts to control overwintering adults (Landwehr et al. 1982). As the distance beetles may fly in search of suitable broodwood is unknown, sanitation must be practised on a large scale to be effective (Lanier and Epstein 1978).

Girdling diseased elm trees to use as trap trees for early summer colonizing beetles may be an effective method of reducing bark beetle populations (Cannon et al. 1982). Once colonization occurs, trees must be removed and burned. Cannon et al. (1982) found 3% fewer elm losses in sites where they used girdling plus sanitation versus sites where sanitation was used alone. Over five years, this translated to a saving of \$5000 per 1000 original elms. As an alternative to girdling, unwanted elm trees may be injected with cacodylic acid (sodium dimethane arsenate) or MSMA (monosodium methane (Gardiner 1979; Lanier 1982; 1989; Pines and arsenate) Westwood in press). These compounds make the tree initially very attractive to breeding beetles, but quickly render the tree unsuitable for brood development (Gardiner 1979; Lanier

1982). However, trees killed with cacodylic acid are less attractive for colonization by H. rufipes than trees with Dutch elm disease (Miller et al. 1986). Trees killed with cacodylic acid are attractive to Scolytus species, but the beetles do not penetrate the bark (O'Callaghan et al. 1984). In Manitoba, H. rufipes breeds in trees treated with MSMA, but not in girdled trees; however, less than 1% of the eggs laid produce viable adults (Pines and Westwood in press). Cut elm logs may also be used as trap logs, provided they are burned or treated with insecticide before any new adults emerge (Lanier 1982; Phillipsen et al. 1986). The trap tree technique is not widely used because of the risk of attracting disease-carrying beetles to nearby trees (Lanier 1982).

The first chemicals used to control elm bark beetles were arsenical compounds (Peacock 1975), until DDT was shown to be more effective (Peacock 1975; Magasi et al. 1993). A variety of chemicals has since been applied to healthy elms to control H. rufipes (Table 2). Although all of these chemicals will kill H. rufipes, the majority are not registered for this use. Most are not used because of their high non-target toxicity Chlorpyrifos (Peacock 1975). currently used most is extensively for several reasons. It is effective for more than one year after treatment, whereas other insecticides are not (Landwehr et al. 1982; Lanier et al. 1984; Phillipsen et al. 1986; Jin unpublished data). Also, chlorpyrifos is effective against beetles boring in or out of overwintering

tunnels (Gardiner and Webb 1980; Landwehr et al. 1982; Lanier et al. 1984; Phillipsen et al. 1986). In addition, chlorpyrifos prevents successful emergence of adults from cut elm when applied either before or after colonization (Lanier et al. 1984; Phillipsen et al. 1986). Methoxychlor suppresses twig crotch feeding better than chlorpyrifos, although it is less effective against H. rufipes than S. multistriatus (Gardiner and Webb 1980; Lanier 1982; Lanier et al. 1984). Methoxychlor is also effective for control of overwintering H. rufipes (Buth and Ellis 1982). Permethrin is also effective against H. rufipes and has the advantage of lower nontarget toxicity. However, permethrin, and other pyrethroids, may have very little residual activity (Landwehr et al. 1982; Quattlebaum 1982; Phillipsen et al. 1986). However, Jin (unpublished data) found that cypermethrin had some residual activity and was effective at very low doses.

Insecticides may be applied to the whole tree to suppress beetle feeding, to cut elm to prevent colonization or emergence by adults, or to the basal 2 to 3 m of the trunk to control overwintering adult *H. rufipes* (Gardiner and Webb 1980). Some researchers believe that spraying tree crowns has little effect on the transmission of Dutch elm disease (Lanier 1982), mainly due to inadequate coverage (Peacock 1975; Perumal et al. 1982). Tests to identify a suitable systemic insecticide have failed, mainly because doses high enough to kill bark beetles were toxic to the trees and other

nontarget organisms (Peacock 1975; Lanier and Epstein 1978). In Manitoba, basal spraying of chlorpyrifos is the only insecticidal portion of the Dutch elm disease management program (Nixon, personal communication).

A variety of biological control agents has been tested against H. rufipes. These include predators such as birds, insects, mites and nematodes, and parasites such as bacteria and fungi (Campana and Stipes 1981). Although some natural enemies had potential in laboratory and field trials, few cause sufficient beetle mortality or reduction in Dutch elm disease transmission for use in practical control programmes. Possible biological control agents tested include Neoplectana carpocapsae Weiser, a nematode (Tomalak and Welch 1982); Phomopsis oblonga, a fungus (Webber 1982); Spathius canadensis Ashmead, a braconid wasp (Kaston 1939; Peacock 1975); the mites, Pediculoides dryas Vitzthum (Kaston 1939; Peacock 1975) and Pymotes scolyti (Ouds.) (Lanier and Epstein 1978); a variety of clerid beetles, most commonly Enoclerus nigripes Say (Kaston 1939; Peacock 1975; Lanier and Epstein 1978); and Lonchaea polita Say, an arboreal lonchaeid fly (Kaston 1939; Peacock 1975). Mortality of H. rufipes due to predators and parasites rarely exceeds 10 to 20% in natural systems (Kaston 1939). Little is known about the potential for augmentation, but any successes in the laboratory have not translated to population reductions in the field, likely because predation and parasitism probably reduce intraspecific competition,

allowing greater survival of uninfected offspring. However, the effectiveness of these natural controls is enhanced by sanitation, since sanitation concentrates the beetle population (Lanier and Epstein 1978).

Mass pheromone trapping using S. multistriatus pheromone has not been successful for control of H. rufipes. Even though beetles are attracted to these sticky traps and large numbers of adults are trapped, there seems to be no diminution of the number of beetles in the next generation (Lanier 1982). Scolytus multistriatus pheromone traps are useful, however, for monitoring general levels of bark beetle populations and periods of activity.

Placing sticky bands around the lower trunks of healthy elm trees may catch many of the adult *H rufipes* as they come down the tree to overwinter at the base. The effectiveness of sticky bands for beetle control is unproven (Gardiner 1981; Buth and Ellis 1982; Gadawski and Robbie-Draward 1993). It appears that effectiveness is influenced by the height of the bands, size of bands, and time of placement. More research is needed to determine effectiveness.

To date, elm breeding programs have been focused on breeding resistance to the fungal pathogen. However, it is possible to breed for resistance to the vector either alone or in conjunction with resistance to the fungus (Heybroek 1993). Resistance could be in the form of either unattractiveness to the vector beetles or actual toxicity to the beetles.

Differences in attractiveness to beetles among different elm species have been found in the past (Heybroek 1993). Unfortunately, a method of comparing resistance levels in elms to the vector beetles has not yet been developed (Heybroek 1993). In addition, the variability of vector species across the range of Dutch elm disease makes vector resistance of limited value.

In Manitoba, many of these control practices will aid in the reduction of Dutch elm disease transmission. Sanitation of dead and dying elms before new *H. rufipes* adults can emerge is probably the most important. Creating trap trees by injecting MSMA, and insecticides applied to trunks of healthy American elms also will significantly reduce vector populations in Manitoba.

Table 1. Elm (*Ulmus*) species in Manitoba and their relative resistance to Dutch elm disease.

Ulmus Species	Common Name	Relative Resistance ¹
americana L.*	American or	
	White elm	
<i>japonica</i> (Rehd.)	Japanese elm	+
<i>parvifolia</i> Jacq.	Chinese elm	++
pumila L.	Siberian elm	++
<i>rubra</i> Muhl.	Slippery or	-
	Red elm	
thomasii Sarg.	Rock elm	-

*species found naturally within Manitoba, others have been introduced ¹- = none, + = some, ++ = much,

(adapted from Heybroek 1981; Webber and Brasier 1984)

Insecticide	$Class^1$	Overwintering Control ²	Feeding Suppression ²
carbaryl	С	+	+
carbofuran	С	?	+
chlorpyrifos*	OP	+	+
lindane	OC	?	+
methoxychlor*	OC	+	+
parathion	OP	?	+
pyrethroid	В	+	+

 ^{1}C = carbamate OP = organophosphate OC = organochlorine B = botanical²+=control ?=unknown (Peacock 1975; Lanier and Epstein 1978; Landwehr et al. 1982; Phillipsen et al. 1986; Jin unpublished data)

* chemicals currently in use in Manitoba

Insecticides potentially effective against Table 2. Hylurgopinus rufipes.

MATERIALS AND METHODS

Emergence Traps

In April 1992, nine healthy American elm trees of various sizes, were selected at the University of Manitoba Glenlea Research Station, Glenlea, MB. Eight of these trees were located in the riverbank bush, and one was located on an adjacent boulevard. On 25 April 1992, emergence traps were placed on the bottom 1.5 m of the trunk of each tree using a design based on Glen (1976) (Figure 1). Each trap divided the trunk into four sections: 0 to 37 cm, 37 to 75 cm, 75 to 112 cm, and 112 to 150 cm above the ground. Each section had trap jars on the north and south sides. North and south were selected as this was the direction the river flowed at this Trap jars were emptied twice each week from 1 May location. to 31 July, 1992, and the H. rufipes counted. On 1 August, the emergence traps were removed, and four of the trees were On each of these four trees, entrance holes were examined. located and the surrounding bark removed with a pocket knife to see if beetles were still in their overwintering tunnels, or if larval galleries had been formed.

Weather information for this period was obtained from the Environment Canada Weather Station at the University of Manitoba Glenlea Research Station.

Comparison of Siberian and American Elms

In fall 1992, three sites where Siberian and American elms coexist were selected. All sites were within 5 km of the Winnipeg city limits (Table 3). At each site ten Siberian and ten American elms were selected and the diameter at breast height (DBH) of each tree measured. In addition, the closest distance between Siberian and American elms was measured for each site. For site S1, the distance between each Siberian elm and its nearest American elm neighbour was measured.

Weekly counts of entrance holes were made in the bottom 35 cm of the trunk of each sample tree from 23 September to 30 October, 1992. The seasonal accumulation of holes was calculated by subtracting the initial hole count from the final hole count. The area sampled was calculated using the formula for the surface area of a cylinder (Area = Height * Circumference) (Selby 1970), where height equals 35 cm. The seasonal accumulation of holes was converted to density for analysis. Data were analysed using multivariate analysis of variance (Wilkinson 1990).

Hole Counts in American Elms - Fall 1992

In August, 1992, stands containing healthy American elms were selected near Dauphin, MB. (Table 4; Figure 2). All sites were located along the Wilson River. Other tree species

present at each site included bur oak (Quercus macrocarpa Michx.), green ash (Fraxinus pennsylvanica Marsh.), and Manitoba maple (Acer negundo L.). Dauphin was chosen because at the start of the study, Dutch Elm Disease had only recently been found there: thus there remained a large number of healthy trees (Westwood 1990). Healthy American elm trees of various sizes within each site were randomly selected (Table 4). For each sample tree, diameter at breast height (DBH) and the area of any root flare (Area = Length of Root Flare * Distance Across the Base * 0.5) (Selby 1970) were recorded.

Entrance holes in the bark were counted at weekly intervals from 12 September to 7 November, 1992 to determine the overall pattern of hole accumulation. Hole counts were made in sections at four different heights above the ground, 0 to 25 cm, 55 to 80 cm, 110 to 135 cm, and 165 to 190 cm, and each segment was divided into north, south, east, and west White plastic string was permanently tied onto quadrants. the tree to ensure the same areas were sampled each week The area of each sample section was measured (Figure 3). [Area = 0.5(Top Length + Bottom Length) * Height] (Selby 1970), where height equals 25 cm. The overall seasonal accumulation of entrance holes was calculated by subtracting the initial hole count from the highest of the last two hole counts. This method was chosen because on the last sample date snow obscured some of the holes, and so the final hole count on some trees was not the largest.

Weather information for this period was obtained directly from the records of Environment Canada's Dauphin Weather Office.

Bark Dissections - Spring 1993

On 6 April, 1993, eleven of the sampled American elm trees from Dauphin were removed from two riverbank sites; five trees were removed from site ST1 and six trees from site ST2 (Figure 2). Trees were cut down and the sections which had been sampled during the fall were separated from the remainder of the tree using a pruning chainsaw. One hundred and fiftytwo samples were immediately wrapped in black plastic garbage bags, brought back to the laboratory at the University of Manitoba and stored at 5° C.

One hundred and forty-two samples were dissected in random order during the period from 25 April to 15 June, 1993. Bark was removed using a wood chisel. Plexiglass[®] was used to surround the log as it was dissected, in order to catch any beetles which may have come off the bark as it was being removed. In addition, the sample bags were checked for any beetles which may have fallen off during transportation and storage. However, very few beetles were found off the bark of a sample. In most cases, the beetles had to be teased off the bark with a paintbrush or the pointed end of a pair of forceps. The numbers of living and dead *H. rufipes*, and the number of overwintering tunnels in each sample were recorded. The remaining 10 samples were not dissected until September, 1993. These samples were not included in any calculations involving the numbers of living beetles.

Hole Counts and Bark Dissections - Fall 1993

The two riverbank sites at Dauphin from which trees had been removed the previous spring, ST1 and ST2, were selected for sampling during the fall of 1993 (Figure 2; Table 4). Entrance holes were counted in the same sample units as the previous year on the sample trees remaining in each site. Holes were counted four times from 5 September to 15 November, 1993 to determine the overall seasonal accumulation of holes. The seasonal accumulation of holes was calculated by subtracting the initial hole count from the final hole count.

On 22 November, 1993, eleven of these trees were removed (five from site ST1, six from site ST2) and the sample units brought back to the lab for dissection as before. In addition, six American elm trees were felled from the University of Manitoba Glenlea Research Station, Glenlea, MB (site ST7), where the *H. rufipes* population was very high. Sections at the same height ranges as those used in Dauphin were removed from the felled trees at Glenlea, and returned to the laboratory for dissection. Dissections occurred from 24 November, 1993 to 15 January, 1994.

Statistical Methods

Statistical analyses were performed using SYSTAT (Wilkinson, 1990). Most data were analysed using analysis of variance. Values of accumulated entrance holes, overwintering beetles, and tunnels were converted to density (numbers per 100 cm²) before analysis. Because of changes in *H. rufipes* population densities between years, each site/year combination was treated as a separate site for analysis (*e.g.* site ST1 in 1992 and site ST1 in 1993 are considered separate sites). Where more detailed analyses were performed, they are described in the pertinent results section.

Site	$Location^1$	Size Rang	je²	Distance ³
		Siberian	American	
S1	East	20.4 to 36.3	15.6 to 26.7	1.3
S2	West	11.7 to 23.5	23.5 to 46.2	58.0
S3	South	7.6 to 26.4	11.1 to 38.2	185.0

Table 3. Site information for comparison of entrance holes in Siberian and American elms near Winnipeg, MB.

¹Relative to Winnipeg city limits. ²Measured as diameter at breast height(cm). ³Minimum distance between the Siberian and American elms (m).

Site ¹	Site Type ²	Number of Elms	Size Range ³
ST1	Natural	15	7.0 to 47.1
ST2	Natural	18	5.1 to 35.7
ST3	Natural	15	7.6 to 41.4
ST4	Planted	10	5.4 to 41.1
ST5	Planted	10	13.4 to 35.7
ST6	Planted	20	15.6 to 31.5
ST7	Natural	6	8.0 to 39.1

Table 4. Site information for American elms in Dauphin and Glenlea, MB.

¹ST1 TO ST6 near Dauphin, MB; ST7 at University of Manitoba Glenlea Research Station. ²Natural = natural riverbank; Planted = planted in a yard or

shelterbelt. ³Measured as diameter at breast height (cm).

Figure 1. Photo of a sample emergence trap used at the University of Manitoba Glenlea Research Station during the spring 1992.



Figure 2. Location of research sites of American elms near Dauphin, MB for 1992 and 1993.



Figure 3. Photo of a sample American elm showing the division into sampling units.



RESULTS

Emergence Traps

The numbers of *H. rufipes* collected on each tree are summarized in Appendix 1. Only 95 beetles were collected in the traps, 80 from the riverbank elms, and 15 from the boulevard elm. Analysis of variance showed no significant difference among the numbers collected at each height (F=.14; d.f.= 3,32) or among the numbers of beetles per tree on the boulevard or riverbank (F=0.9; d.f.=1,34). The numbers of beetles collected were much smaller than expected, considering previous studies of dust pile counts and bark dissections at that location (Ellis, unpublished data), and it was concluded that the traps did not function properly. No further analyses were performed.

On the trees examined closely, there were no adult beetles or larval galleries found. However, there were large numbers of overwintering holes and empty tunnels. These holes and tunnels were at greatest density near the ground.

Comparison of Siberian and American Elms

The mean density of entrance holes was less on the Siberian elms than that on the American elms for each site (Table 5). Although the relationship between the two values is linear and has a r^2 -value of 0.94 (Figure 4), the number of samples was too small to allow the density of entrance holes on Siberian elms to be accurately predicted from the density of entrance holes on the American elms.

Analysis of variance for the minimum distance between the American and the Siberian elms in each site, showed no significant effect on the density of entrance holes (F=0.2; d.f.=1,2). However, when I looked at site S1, the only site where the distance between each Siberian elm and its nearest American elm neighbour was measured, the density of entrance holes was significantly influenced by the proximity of an American elm (F=11.0; d.f.=1,8; p<0.05) (Figure 5).

The mean tree sizes for each tree species at each site are summarized in Table 5. Within each site there was little variation in size for each tree species because they were planted at the same time in a shelterbelt. Thus, it is not possible to determine from this data if tree size has any effect on the accumulation of entrance holes in Siberian elms.

In April, 1993, two and three overwintering *H. rufipes* were removed from each of two trees in site S1. All five were alive.

S1 A 25.6 (1.6) 1.19 (0.17) S1 S 34.9 (2.4) 0.37 (0.08) S2 A 40.3 (2.1) 0.24 (0.05) S2 S 16.2 (1.2) 0.08 (0.02)	Site	$Species^1$	DBH (cm)	Holes/100cm ²
S1 S 34.9 (2.4) 0.37 (0.08) S2 A 40.3 (2.1) 0.24 (0.05) S2 S 16.2 (1.2) 0.08 (0.02)	S1	A	25.6 (1.6)	1.19 (0.17)
S2 A 40.3 (2.1) 0.24 (0.05) S2 S 16.2 (1.2) 0.08 (0.02)	S1	S	34.9 (2.4)	0.37 (0.08)
S2 S 16.2 (1.2) 0.08 (0.02)	S2	A	40.3 (2.1)	0.24 (0.05)
	S2	S	16.2 (1.2)	0.08 (0.02)
S3 A 22.8 (2.2) 0.35 (0.07)	S3	А	22.8 (2.2)	0.35 (0.07)
S3 S 18.1 (2.0) 0.19 (0.04)	S3	S	18.1 (2.0)	0.19 (0.04)

Table 5. Mean (\pm S.E.) tree size and density of accumulated entrance holes for American and Siberian elms.

¹ A = American elm; S = Siberian elm.

Figure 4. The relationship between the density of accumulated entrance holes on Siberian and American elms in three sites (S1, S2, S3) in Winnipeg, MB.



Figure 5. Relationship between the density of accumulated entrance holes in Siberian elms and their distance from an American elm for site S1 in Winnipeg, MB.



1. I. I.

American Elms

Weekly Accumulation of Holes

The accumulation of entrance holes was relatively constant throughout the sampling period for all heights except ground to 25 cm (Figure 6). In this height range, there was an increase in the weekly accumulation of holes in the weeks 10 October, 1992. At this time, daily minimum after temperatures were mostly below freezing, and daily maximum temperatures below 20°C (Figure 6). There is no apparent difference between the patterns of entrance hole accumulation in natural and planted stands of American elm (Figure 6). Several more weeks of sampling would have been useful to determine when accumulations of holes diminished. Unfortunately, snow buried the base of sample trees by 7 November, 1992.

Figure 6. Mean (±S.E.) weekly accumulation of entrance holes for each height range on natural and planted American elm trees in Dauphin, MB - Fall 1992; and minimum and maximum temperatures in Dauphin for the same time period.


DATE

Effect of Height Above the Ground

For analysis of the effect of height, data were transformed to give the proportion of accumulated entrance holes, overwintering beetles and tunnels in each height range for each tree. This was done to eliminate differences due directly to different numbers of *H. rufipes* per tree in the different sites. Trees with no entrance holes, overwintering beetles or tunnels were not included in the analyses.

In the counts done in Dauphin, MB in 1992 and 1993, I found that overall 51% of the accumulated entrance holes were in the 0 to 25 cm height range, and approximately 17 % were found in each of the other height ranges (Figure 7). The 0 to 25 cm height range had a significantly greater proportion of entrance holes than the other height ranges (F=312.2;d.f.=3,412; p<0.001), but there was no significant difference in the proportions of entrance holes in the other three height ranges (F=1.3; d.f.=2,309). There were no significant interactions between height and site for entrance holes in natural stands (F=0.7; d.f.=3,212) or in all sites combined (F=1.1; d.f.=15,392). Stand type (i.e. planted versus natural) did not interact significantly with the proportion of entrance holes at each height (F=1.2; d.f.=3,408) (Figure 8). Therefore, the proportion of accumulated entrance holes for each height range was not affected by site, year or stand type.

In the bark dissections from ST1, ST2, and ST7 in spring

and fall 1993, 57% of the overwintering tunnels were found in the 0 to 25 cm height range, 17% in the 55 to 80 cm height range and approximately 13% in each of the next two height ranges (Figure 7). There was a decline in proportion of overwintering tunnels over height; the 0 to 25 cm height range had a significantly higher proportion than the other three (F=274.3; d.f.=3,108; p<0.001), the 55 to 80 cm range was significantly greater than the higher two (F=4.9; d.f.=2,81; p<0.01), but the height ranges 110 to 135 cm and 165 to 190 cm were not significantly different (F=.09; d.f.=1,54) (Figure 7). There was no significant interaction between the proportion of overwintering tunnels at each height and site (F=0.5; d.f.=4,102), thus the proportion of overwintering tunnels at each height was not affected by site or year.

Ninety-six percent of the overwintering *H. rufipes* collected from the bark dissections in spring and fall 1993 were found in the 0 to 25 cm height range, 2% in the 55 to 80 cm height range and 1% in each of the other two height ranges (Figure 7). The 0 to 25 cm height range had a significantly greater proportion of overwintering beetles than the other height ranges (F=5.7; d.f.=3,96; p<0.001) and there was no difference in the proportions of overwintering beetles among the other three height ranges (F=1.6; d.f.=2,72). However, only 1 out of 19 in the spring 1993 and 2 out of 57 in the fall 1993 of the *H. rufipes* found above 25 cm from the ground were alive. There was no significant interaction between the

proportion of overwintering beetles at each height and site (F=0.04; d.f.=4,90), thus the proportion of overwintering beetles found in each height range was not affected by site or year.

Although the distribution of overwintering tunnels and accumulated entrance holes appear similar (Figure 7), they are significantly different ($Chi^2=56.4$; d.f=3; p<0.001). The distribution of overwintering beetles on a tree, however, was very different than that of overwintering tunnels or accumulated entrance holes ($Chi^2=1808.7$; d.f.=3; p<0.001).

Less than 4% of the total number of *H. rufipes* collected were from above 25 cm, and of these less than 4% were alive. Also, during the dissection, I observed that the majority of the overwintering beetles and tunnels were found in the lower half of the 0 to 25 cm samples. Thus, the remainder of analyses were performed only on data from the 0 to 25 cm height range.

Figure 7. Mean proportion $(\pm S.E.)$ of accumulated entrance holes, overwintering *H. rufipes*, and tunnels observed for each height above the ground in natural American elms in Dauphin, MB pooled over 1992 and 1993.



Figure 8. Mean percentage $(\pm S.E.)$ of accumulated entrance holes observed for each height above the ground in natural and planted American elms in Dauphin, MB during the fall 1992.



Effect of Aspect

Analysis of variance for the density of accumulated entrance holes by compass aspect from ground to 25 cm in all Dauphin sites in fall 1992 and 1993 was significant (F=4.0; d.f.=3,168; p<0.01). Although no interaction of aspect with site was evident (F=0.9; d.f.=9,168), there appears to be no constant effect of aspect among sites (Table 6). There was no relationship between the density of accumulated entrance holes and the direction to the river at each site. The orientation of the river had neither consistently the highest or the lowest density of accumulated entrance holes.

Aspect had no significant effect on the densities of overwintering *H. rufipes* (F=0.1; d.f.=3,69), or tunnels (F=0.4; d.f.=3,69) observed. In addition, there was no interaction between aspect and site for overwintering beetles (F=0.9; d.f.=12,69) or tunnels (F=0.2; d.f.=12,69). Analysis of accumulated entrance holes restricted to the samples which were dissected was still significant for aspect (F=3.0; d.f.=3,53; p<0.05), and again showed no interaction with site (F=0.6; d.f.=9,53).

If exposure had an influence on the numbers of beetles attempting to overwinter on each aspect, we would expect to see it most obviously between the two rows of the shelterbelt in site ST6. Thus, this site was analysed individually. Aspect was not significant. The results of an analysis of variance for density of entrance holes at site ST6 are as follows: aspect (F=1.2; d.f.=3,72); row (F=0.9; d.f.=1,72); aspect * row (F =0.7; d.f.=3,72).

Site	Perc	Percentage ¹		Direc	Direction ²	
	N	S	Е	W		
ST1-92	22	21	32	25		SE
ST1-93	15	29	29	27		SE
ST2-92	25	26	30	20		N
ST2-93	31	26	24	19		N
ST3-92	19	31	32	18		S
ST4-92	34	21	30	15		S
ST5-92	31	18	23	28		SW
ST6-92	24	25	21	29		SW
POOLED	25	25	28	22		

Table 6. Mean percentage of accumulated entrance holes for each compass aspect in the ground to 25 cm height range for all sites in Dauphin, MB - Fall 1992 and 1993, and the direction to the river for each site.

 $^{1}\text{Percentage}$ of total accumulated holes found at each aspect; N=north, S=south, E=east, W=west. $^{2}\text{Direction}$ to the river.

Effect of Tree Location

The density of accumulated entrance holes is significantly affected by where the tree is situated. Analysis of variance using a nested design for planted sites of American elms and their adjacent natural sites shows that both stand type and stand location are significant (F=22.6; d.f.=1,254; p<0.001: F=23.8; d.f.=1,254; p<0.001 respectively) (Table 7). However, there was no interaction between stand type and location (F=2.0; d.f.=1,254). In each location, the planted stands had significantly fewer entrance holes than the natural stands (Table 7). Remaining analyses were performed on sites containing natural riverbank American elms only.

Table 7. Mean (±S.E.) accumulated entrance holes per 100 $\rm cm^2$ from ground to 25 cm in planted stands of American elms and their adjacent natural stands in Dauphin, MB.

Site	$Location^1$	Stand Type ²	Holes/100cm ² (±S.E.)
ST2	1	Natural	2.17 (0.024)
ST5	1	Planted	1.17 (0.016)
ST6	1	Planted	1.39 (0.008)
ST3	2	Natural	1.31 (0.016)
ST4	2	Planted	0.85 (0.019)

¹see Figure 1. ²Natural = natural riverbank; Planted = planted in yard or shelterbelt.

Effect of Tree Size

Ninety-five percent of both overwintering *H. rufipes* and tunnels from the dissected samples were found in trees with DBH greater than 13 cm. No living beetles were found on trees smaller than 8 cm DBH and no beetles were found on trees less than 7 cm.

Analysis of variance showed that tree size had a significant effect on the density of accumulated entrance holes, overwintering beetles and tunnels (Table 8). An examination of whether the regressions for tree size were identical in all sites was done by testing the hypothesis that site and site * DBH interaction were simultaneously nonsignificant in all three cases (Table 8). However, graphical analysis indicated that this relationship was not linear. An iterative process was used to fit the logistic model,

Mean Density = $\frac{A}{1+b(\rho^{DBH})}$

and in all cases this was a good fit (Table 9). An example of the logistic model fitted to overwintering beetles in site ST2-93 is shown in Figure 9. Figures 10, 11 and 12 depict the relationship between densities of accumulated holes, overwintering beetles and overwintering tunnels to tree size. To make comparisons between sites, a logit transformation was used to adjust for different population densities. Each mean

69

density was divided by the maxima from the iterative process to get a value between 0 and 1 (P in the logit equation). The logit transformation was performed on this value (Robertson and Preisler 1992).

$$logit(P) = ln(\frac{P}{1-P})$$

The resultant logit values were then subjected to the same analysis of variance as for the untransformed data, including the same test of hypothesis. Only DBH was significant (Table 8). Thus the effect of tree size was consistant between sites and years. Table 8. Relationship of the density of accumulated entrance holes, overwintering *H. rufipes*, and tunnels from ground to 25 cm to tree size and the interaction between tree size and site on American elm trees in Dauphin and Glenlea, MB.

Dependent	Independent	Untransformed		Logit	
variable	variables ¹	transform		ation	
		F-value	d.f.	F-value	d.f.
Holes	DBH	25.9***	1,39	8.7** 1,3	
	DBH*SITE&SITE	4.0*	2,39	0.9	2,33
Beetles	DBH	15.6***	1,21	29.6***	1,11
	DBH*SITE&SITE	6.3**	4,21	0.04	4,11
Tunnels	DBH	19.0***	1,21	29.4**	1,6
	DBH*SITE&SITE	12.2***	4,21	0.6	4,6

*p<0.05, **p<0.01, **p<0.001. ¹DBH*SITE&SITE tests whether the identical in all sites. DBH regressions were Table 9. Results of the iterative process to fit data to the model Mean Density = A / $(1 + b (\rho^{DBH}))$ for accumulated entrance holes, overwintering *H. rufipes*, and tunnels from ground to 25 cm on American elm trees in natural riverbank sites in Dauphin and Glenlea, MB.

Site	Observed	Values					
	Variable	А	b	ρ	r ²		
ST1&2-92	Holes	3.9	4.1	0.92	0.86		
(Pooled)	Beetles	1.4	0.73E+10	0.20	0.91		
	Tunnels	6.5	58.9	0.77	0.88		
ST1-93	Holes	2.8	655.1	0.57	0.96		
	Beetles	3.9	0.49E+11	0.19	0.99		
	Tunnels	20.0	8851.2	0.54	0.98		
ST2-93	Holes	3.9	183.1	0.59	0.96		
	Beetles	11.4	0.42E+12	0.07	0.93		
	Tunnels	22.4	750.4	0.54	0.97		
ST7-93	Beetles	23.1	756.6	0.65	0.99		
	Tunnels	46.7	2135.7	0.46	0.97		

 $= \{\xi_i\}_{i=1}^{N} \in \mathbb{N}^{N}$

73

Figure 9. The logistic model fitted to the density of overwintering *H. rufipes* for the ground to 25 cm height range in site ST2 - Fall 1993.



Figure 10. Relationship between the density of accumulated entrance holes and tree size for the height range ground to 25 cm in natural American elms in Dauphin, MB - Fall 1992 and 1993.



Figure 11. Relationship between the density of overwintering adult *H. rufipes* and tree size for the height range ground to 25 cm in natural American elms in Dauphin and Glenlea, MB -Spring 1993 and Fall 1993.



Figure 12. Relationship between the density of overwintering tunnels and tree size for the height range ground to 25 cm in natural American elms in Dauphin and Glenlea, MB - Spring 1993 and Fall 1993.



Effect of Root Flare

Regression analysis of root flare area was completed for samples with root flare area greater than zero and for all samples in sites ST1 and ST2 in 1992 and 1993. The area of the root flare did not significantly affect densities of accumulated entrance holes, overwintering beetles, or tunnels (Table 10). The analysis was repeated for the percent of the the total area of the ground to 25 cm height range which was root flare. Again, the root flare did not have a significant effect on the densities of accumulation of holes (F=3.7; d.f.=1,191), overwintering beetles (F=1.8; d.f.=1.72), or tunnels (F=1.7; d.f.=1.72). Table 10. Relationship between the area of the root flare and the density of accumulated entrance holes, overwintering H. rufipes, and tunnels on American elms in natural riverbank sites in Dauphin, MB - Fall 1992, Spring and Fall 1993.

Observed	All Sample	Area Root > 0			
Variable	F-value(d.f.)	P-value	F-val	ue(d.f.)	P-value
Holes	1.5 (1,190)	0.22	0.12	(1,29)	0.74
Beetles	1.7 (1,71)	0.19	2.0	(1,10)	0.19
Tunnels	1.5 (1,71)	0.23	0.5	(1,10)	0.48

Overwintering Survival

Unfortunately, the same population of H. rufipes was not followed through a complete winter. However, samples dissected in spring 1993 contained beetles which had already overwintered and those in fall 1993 contained beetles which had not yet overwintered. Thus some generalities may be inferred. It appears that overwintering survival is affected by the size of the tree. No living beetles were found on trees of DBH 8 cm or smaller in the spring of 1993: however, the tree with a DBH of 8 cm in the fall of 1993 had approximately 75% of the beetles alive (Figure 13). In addition, trees with a DBH of 9 cm to 15 cm had only 36% of the beetles alive in the spring 1993, whereas in fall 1993 80% of the beetles in trees within this size range were living (Figure 13). Above a DBH of 17 cm, overwintering mortality appears low, with 80% alive in the spring of 1993 and 87% alive in the fall of 1993 (Figure 13).

Above the ground to 25 cm height range, the percentage of *H. rufipes* which were alive was very low. In the fall, only 4% (2 of 57) and in the spring, only 5% (1 of 19) of the beetles recovered were living. The ability of *H. rufipes* to survive the winter at these heights cannot be determined from these data.

Figure 13. The percentage of *H. rufipes* which were alive in relation to tree size when removed from ground to 25 cm in American elm samples - Prior to Overwintering (Fall 1993) and After Overwintering (Spring 1993).



Prediction of Beetles From Accumulated Holes

In the relationship between overwintering H. rufipes and the seasonal accumulation of entrance holes for ground to 25 cm, the slope of the regression was significantly different between the two years (F=6.1; d.f.=1,69; p<0.05). From analysis of residuals, a natural log transformation of the number of overwintering beetles was appropriate (Wilkinson 1990). Regression of the transformed values showed that the significantly different slope was longer no (F=0.18;d.f.=1,62). A test of the hypothesis that both the slope and the intercept were different between the two years was not significant (F=1.4; d.f.=2,62). The pooled relationship between overwintering H. rufipes and accumulated entrance holes is shown in Figure 14. Although the relationship is significant, the r^2 value was only 0.46; thus there is a great deal of variation.

Not enough *H. rufipes* were found above 25 cm from the ground to allow for analysis of the relationship between accumulated holes and overwintering beetles in the other height ranges.

Figure 14. The relationships between the accumulation of entrance holes in the fall and the number of *H. rufipes* overwintering from ground to 25 cm in the trunk of American elms in Dauphin, MB - Fall 1992 and Spring and Fall 1993.



ACCUMULATED ENTRANCE HOLES

DISCUSSION

Emergence Traps

There are several possible reasons why the emergence traps failed to capture H. rufipes as they emerged from their overwintering sites. Beetles may not have been able to locate the exit holes into the collecting jars, or they may have emerged through a different part of the trap, for example the seam of the cloth. It is also possible that the traps were placed on the trees too late to capture emerging beetles. Traps were in place by 25 April, 1992; however, temperatures had reached 15°C by 18 April, 1992. Beetles have not been reported leaving their overwintering tunnels until temperatures reach 20°C (Lanier 1978), but they are capable of becoming active at much lower temperatures (Becker 1935). There were many entrance holes and overwintering tunnels so H. rufipes were present; however, it is possible that these holes and tunnels were from previous years and that the trees had recently become unsuitable for overwintering.

Several other trap types have been used successfully to capture bark beetles emerging from trees. Gara and Vite (1965) used both cloth tents and aluminum surrounds with collecting jars to capture beetles. Unfortunately, both trap types required intensive labour to set up and monitor. Langor and Raske (1987) and Langor and Herger (1993) also

used cloth tents with collecting jars. McClelland et al. (1978) recommended using metal plates with round holes screwed into the bark of the tree, with mesh collecting nets attached. However, this trap design would only work on trees large enough to have a relatively flat sampling surface. It also could not be used to collect beetles at ground level. Swedenborg et al. (1988) used plastic tents coated on the inside with a sticky substance. While these traps caught most of the emerging beetles, they have limited value if one needs healthy beetles for further study. It appears that the best method to collect the bark beetles emerging from a tree depends on several factors: tree size, location on the tree, and future use of collected beetles.

Siberian Elms

Hylurgopinus rufipes is able to overwinter successfully in Siberian elms. I found living *H. rufipes* in Siberian elms in the spring of 1993. However, several conditions are probably needed for this to occur. The Siberian elm must be located close to an American elm. I found that the density of accumulated entrance holes decreased rapidly as the distance from an American elm increased. Also, there must be a high population of *H. rufipes* in the area, as accumulations of holes in Siberian elms were greatest in the site with high *H. rufipes* populations. Hildahl and Wong (1965) probably did not

sample Siberian elms that met these conditions, thus did not find H. rufipes on Siberian elms. Additional research is needed to determine exactly how close the Siberian and American elms need to be in order for beetles to choose to overwinter in a Siberian elm. This distance is probably influenced by population density of both species of elms as well as by beetle populations. It is not known if Siberian elms are subject to the same size limitation of an acceptable overwintering location as small American elms. As Siberian elms have thicker bark than American elms (Webber and Brasier 1984) it is possible that smaller trees would be acceptable. I would currently recommend insecticidal applications for control of overwintering H. rufipes be applied only to Siberian elms that are near American elms in locations with high beetle populations.

American Elms

Weekly accumulation of entrance holes in ground to 25 cm height range during fall 1992 increased as the daily minimum temperature dropped below freezing, on about 10 October, 1992. Buth and Ellis (1982) found increased overwintering activity in Manitoba after 15 September, but did not include weather information. In Minnesota, overwintering activity begins after mid-September (Landwehr et al. 1982). Also, Lanier (1983) noticed that in New York as the temperature drops in
the fall, H. rufipes move from their feeding location to the base of the tree to overwinter. It may be that temperatures below 0°C trigger the movement down the tree to overwinter at the base. The weekly accumulation of entrance holes was constant for the other height ranges. These holes are probably entrances to feeding tunnels. There is no apparent morphological difference between а feeding and an overwintering tunnel (Becker 1937; Kaston and Riggs 1938).

In Manitoba, greater than 94% of the beetles overwinter below 55 cm from the ground. This leaves only 4% of the overwintering H. rufipes recovered from my samples above the ground to 25 cm sample, and only 3 out of 76 of these individuals were alive. In contrast, almost 50% of the total entrance holes and tunnels were observed above 25 cm. Although I did not sample between 25 cm and 55 cm from the ground, I conclude that the majority of the H. rufipes are overwintering within 25 cm of the ground, as I observed that most of the beetles in these samples were in the lower half. These results agree with Landwehr et al. (1982) from Minnesota, Gardiner and Webb (1980) from Manitoba, and Ellis (unpublished data) from Manitoba. In their study, Gardiner and Webb (1980) found that although in Manitoba H. rufipes overwinters in the lower trunk, this was not the case in the Maritimes, Quebec, or Ontario, and that in Manitoba, the beetles seemed to be as close to the ground as possible. They thought that this behaviour may be an adaption to lower winter

temperatures and less snow accumulation. However, the presence of snow around the base of the tree does not affect overwintering survival (Landwehr et al. 1982). It might be informative to try and link the presence of overwintering adult beetles higher up on healthy elms with a high percentage of adults producing a second generation as both of these appear to be indicators of the absence of a true diapause. In these cases, it is likely that the individuals just become quiescent as the temperature drops. This theory is supported by the presence of eggs, pupae and callow adults, which fail to survive the winter (Kaston, 1939; Thompson and Matthysse 1972). Unfortunately, the data are not available to support this hypothesis.

Aspect had no clear effect on the accumulation of entrance holes. The accumulation of entrance holes does not appear to be affected by exposure or the direction to a nearby waterway. Martin (1938) found that the degree of exposure did not affect the colonization of broodwood by *H. rufipes*. Exposure had no effect on the accumulation of entrance holes between the two rows of the shelterbelt, which is where I would expect the most consistent effect to be. There was no consistent effect of the orientation of the river on the accumulation of entrance holes, or numbers of overwintering beetles or tunnels. It may just be that differences in aspect are related to sampling efficiency, particularly if one aspect has greater light penetration through the canopy or a

different amount of moss coverage. The idea of an artifact due to sampling is supported because aspect was not significant for either overwintering *H. rufipes* or for tunnels.

There was a significantly greater accumulation of entrance holes in the natural riverbank sites when compared to their planted neighbours. This supports the hypothesis that overwintering *H. rufipes* prefer shaded areas, rather than open sites (Kaston 1939; Lanier 1978). It also supports the hypothesis that the beetles do not fly very far between emerging from brood galleries and searching for feeding and overwintering sites (Kaston 1939). There would be greater amounts of suitable broodwood in the natural sites than in the planted sites, which, except for the shelterbelt, were subject to pruning.

Ninety-five percent of the overwintering *H. rufipes* and tunnels were observed in trees greater than 15 cm DBH. No living beetles were found in trees smaller than 8 cm DBH, although tunnels were found in these trees. Very few *H. rufipes* were found in trees which were between 8 and 15 cm DBH, and for trees of these sizes overwintering mortality appeared to be high. Ellis (unpublished data) found less than 2 boring dust piles per tree in American elms less than 5 cm DBH in Manitoba. It is possible that smaller trees do not have sufficiently thick bark to support overwintering (Thompson and Matthysse 1972; Lanier 1978), although the reason for needing thick bark is not clear. It is unlikely

that thicker bark provides protection from low temperatures, as overwintering adult H. rufipes are able to survive freezing (Landwehr et al. 1982). One possibility is that thick bark is needed to ensure sufficient penetration before encountering the living tussue, and thus host defence mechanisms. Τf significant source of overwintering dessication is a mortality, it is possible that thick bark and proximity to the ground protect the beetle from the wind. An alternative hypothesis is that thick bark provides protection from flooding, to which many riverbank American elms are subject annually. Hylurgopinus rufipes must not be able to determine bark thickness prior to penetration, since entrance holes and tunnels were observed in smaller trees, but no beetles were found there.

Above a DBH of approximately 15 cm, the density of accumulated entrance holes, overwintering beetles, and tunnels in the ground to 25 cm height range within a given site did not vary. However, the actual densities of these factors on trees greater than 15 cm DBH increased as the beetle population density increased between sites. *Hylurgopinus rufipes* must not prefer trees of different sizes once a minimum size has been reached, as tree size selection by overwintering beetles did not change between the sites and years. However, larger trees do have more overwintering *H*. *rufipes* on them, as they have a greater surface area.

Becker (1935) found H. rufipes overwintering on the root

flare. The root flare may be more attractive to overwintering H. rufipes than the trunk (Pines personal communication). Beetles were found overwintering on the root flare. However, since the area of the root flare had no effect on the densities of accumulated entrance holes, overwintering beetles or tunnels, it is likely that the root flare is not any more or less attractive than the base of the tree. The bark of the flare root may become too thin for successful overwintering at a short distance from the trunk. More research is needed here.

Trees 8 cm to 15 cm DBH are possibly too small for good overwintering survival. In the fall these trees had about 80% living beetles, but in the spring this value had dropped to 35%. Lanier (1978) reported that trees less than 5 cm DBH do not have sufficiently thick corky bark to ensure winter survival. Overwintering beetles on trees greater than 15 cm DBH show good survival as the percentage of beetles living is 87% in the fall and 80% in the spring. Unfortunately, as I did not follow the same group of beetles through one overwintering period, I cannot conclude that overwintering mortality from ground to 25 cm is only 7%. Above the ground to 25 cm level, the percentage living was low, 4% in the fall and 5% in the spring. Survival cannot be determined at these heights as there were not enough beetles found there. Kaston (1939) found that survival of overwintering H. rufipes was greatest in the lower parts of the tree.

Prediction of Overwintering H. rufipes From Accumulated Holes

It may be possible to predict the number of H. rufipes overwintering in a given tree from the accumulation of entrance holes. Unfortunately, the relationship is complex, and the natural log transformation makes prediction difficult. Also, this relationship has a low r^2 value, explaining less than 46% of the variation. The low r^2 reduces the precision of any potential predicted value. I observed that as the population density increased, the proportion of beetles sharing overwintering tunnels with another beetle increased. In one case of very high population density, beetles were observed overwintering not in tunnels, but clustered together in the cracks of the bark. These changes in behaviour by H. rufipes would result in fewer entrance holes per beetle as the population increased. I would not recommend using counts of entrance holes if one needs accurate predictions of the numbers of beetles; however, accumulations of entrance holes could still be used if one wanted only to know which trees at a given location were being used for overwintering.

Comparison with Other Bark Beetle Species

In Manitoba, *H. rufipes* overwinters as an adult below 55 cm from the ground, and most likely below 25 cm from the

ground, on healthy American elm trees. This behaviour is not unusual for bark beetles. Two species of bark beetle which attack elm trees in Europe, Pteleobius vittatus (F.) and P. kraatzi (Eichhoff), overwinter in this location (Wood 1982). A closely allied species, Dendroctonus simplex LeConte (Wood 1982), overwinters at the base of healthy larch trees (Langor and Raske 1987). Hylesinus californicus (Swaine) attacks ash trees, which have a similar distribution to American elm (Langor and Hergert 1993). This species also overwinters at the base of healthy trees (Langor and Hergert 1993). In addition, H. californicus, like H. rufipes, exhibits a change in the number of generations per year in different geographical locations, and can be found overwintering as either a larva or an adult in the southern parts of its range, but only as an adult in the north (Langor and Hergert 1993).

Implication for Vector Management

The current practice for overwintering control of *H*. *rufipes* in Manitoba is to spray all elm species and sizes to a height of 2 m. The results presented here indicate that insecticide applications could be limited to the bottom 25 cm of American elms greater than 15 cm DBH and still provide greater than 95% control. Few beetles were found above the ground to 25 cm height range, and less than 4% of these were living. Also, less than 5% of the beetles in the ground to 25

cm height range were found on trees smaller than 15 cm. Limiting insecticidal applicantion in this manner would directly result in reduced costs for insecticides and labour. An added benefit would be a reduction in the risk of environmental contamination and non-target toxicity. Siberian elms only need to be treated when American elms are nearby and the populations of *H. rufipes* are near epidemic levels. Insecticides should be applied before the temperatures drop below 0°C, in order to catch the beetles as they first enter their overwintering tunnels. However, if this period is missed, some insecticides are effective against beetles leaving their overwintering tunnels (Gardiner and Webb 1980; Landwehr et al. 1982; Lanier et al. 1984; Phillipsen et al. 1986).

As a result of this thesis research, I would currently recommend that insecticides applied against overwintering adult *H. rufipes* be restricted to the bottom 25 cm of healthy American elms greater than 15 cm DBH. Siberian elms should only be treated when they occur in conjunction with American elms in locations where *H. rufipes* is abundant. Further work is needed to determine overwintering behaviour of *H. rufipes* in planted American and Siberian elms, as well as its survival in these locations.

CONCLUSIONS

- Hylurgopinus rufipes is able to overwinter successfully on Siberian elms, but is only found on Siberian elms planted close to an American elm in areas where the population of *H. rufipes* is very high.
- 2. Hylurgopinus rufipes prefers to overwinter in trees greater than 15 cm DBH. Above this tree size the density of overwintering beetles does not change. No beetles were found overwintering successfully on trees less than 8 cm DBH.
- 3. Hylurgopinus rufipes prefers to overwinter in natural riverbank American elms rather than those planted in more open areas.
- 4. Hylurgopinus rufipes overwinters within 55 cm of the ground, and probably within 25 cm of the ground, on the trunks of healthy American elms.
- 5. The number of *H. rufipes* overwintering on a given tree may be estimated from the seasonal accumulation of entrance holes using the following equation: Ln (Beetles) = 0.91 + 0.09 (Accumulated entrance holes). However, this relationship has relatively low predictive precision and should be used only as a general guide.

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Location ¹	DBH(cm)	Number c	of Beetles	at Each	Height
		0-37	38-75	76-112	113-150
BLVD	17	9	3	3	0
RVBK	5	1	2	0	2
RVBK	6	2	3	2	6
RVBK	7	0	0	0	0
RVBK	9	2	0	0	0
RVBK	10	5	1	6	4
RVBK	12	0	0	4	2
RVBK	14	3	4	7	2
RVBK	38	4	7	4	7
	TOTAL	26	20	26	23

Appendix 1. Hylurgopinus rufipes collected from emergence traps at Glenlea, MB - Spring 1992

¹ BLVD = boulevard, RVBK = riverbank ² height ranges are in centimetres from the ground