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THE LIFE HISTORY OF PINACODERA LIMBATA DEJEAN AND
PINACODERA PLATICOLLIS SAY (COLEOPTERA: CARABIDAE)
IN OAK FORESTS
IN MICHIGAN

presented by

Joseph M. Mahar

has been accepted towards fulfillment
of the requirements for

Master of Science degree in Entomology

A handwritten signature in cursive script, likely of the Major professor, written over a horizontal line.

Major professor

Date 7 Aug 1978

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ABSTRACT

THE LIFE HISTORY OF PINACODERA LIMBATA DEJEAN AND
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Two species of the North American, lebiine genus of Pinacodera, P. platicollis and P. limbata were studied in the oak-dominated Manistee National Forest of Lower Michigan. Nine different trapping techniques were utilized to sample for these species. Adults were collected from the litter and from trees, while larvae were collected only from the litter. P. platicollis appears to be a spring breeder while P. limbata is a summer breeder, both with apparent diapausing larvae. Crepuscular activity was found in adults of both species with most nocturnal activity occurring in the canopy.

Other lebiine carabids found in the course of the study were Metabletus americanus, Cymindis cribicollis, C. neglecta, C. pilosa, Lebia bivittata, L. viridis, Plochionus timidus, and Dromius piceus. After the Pinacodera species, D. piceus was the most abundant lebiine carabid. Larvae and one pupa of D. piceus were taken from the trees. One known larva of Cymindis neglecta was collected from the litter.

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Many people can take some credit for the completion of this study. Chronologically, the three most important are Dr. William Wallner, who introduced me to forest entomology and graduate school, Dr. Fred Stehr, who replaced Wallner and was my advisor for the greatest length of time and Dr. Gary Simmons, who provided support, allowing his time, energy and equipment to be used towards the completion of this project.

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TABLE OF CONTENTS

	PAGE
LIST OF TABLES	v
LIST OF FIGURES	vii
INTRODUCTION	1
METHODS	5
Plots and Plot Conditions	5
Plots	5
Plot Conditions	5
Trapping Methods	7
Fixed Traps	7
Malaise Traps	7
Sticky Boards	7
Pitfall Traps	9
Blacklight	11
Winter Soil Sampling	11
Movable Trapping	11
Pyrethrum Spraying	11
Night Collecting	11
Bark Stripping	12
Hand Collecting	12
Biology Investigations	12
Feeding Trials	12
Rearing Experiments	12
Winter Cage	13
Dispersal Experiment	13
Dissection of Females	13
Larval Rearing	14
Temperature Recording	14
Soil Testing	14
Results	15
Data prior to September - 1975	15
Pyrethrum Spray Results - 1976	15
Bark Stripping - 1976, 1977	15
Dispersal Experiment - 1976	19
Hand Collecting - 1976	19
Soil Sampling - 1976, 1977, 1978	21
Night Collecting - 1976, 1977	21
Malaise Traps - 1976, 1977	22

	PAGE
Sticky Board Traps - 1976, 1977	22
Blacklight - 1976, 1977	24
Pitfall Traps - 1976, 1977	24
Larval Rearing - 1977, 1978	24
Feeding Trials - 1976, 1977	31
Dissection of Females - 1976, 1977	31
Observed Nocturnal Feeding	32
Predation	33
Associated Lebiine Carabids	33
Life Cycle of <u>P. platicollis</u> and <u>P. limbata</u> - A Summary .	33
Discussion	36
Determination of Life Stages	36
The Types of Life Cycles	37
Daily and Seasonal Activity	38
Preferred Sites	40
Predation	40
The Role of <u>Pinacodera</u> Species	41
Competition	41
Areas for Continued Research	42
APPENDIX	43
1. Description of the <u>Pinacodera</u> species	43
2. Stand characteristics of the plots	44
3. Soil characteristics of the plots	45
LITERATURE CITED	46

LIST OF TABLES

TABLE	PAGE
1. Means of <u>Pinacodera platicollis</u> , <u>P. limbata</u> and <u>Dromius piceus</u> taken from spray samples from red and white oaks in the Manistee National Forest around Baldwin, Michigan, 1976	18
2. The number of <u>Pinacodera limbata</u> recovered from the second spraying of four pairs of trees near the Branch Pole plot in the Manistee National Forest northwest of Baldwin, Michigan, August, 1976	18
3. The ground population of <u>Pinacodera platicollis</u> as determined from 5 weekly transects made in the Branch Mature and Branch Pole plots in the Manistee National Forest, Baldwin, Michigan, April and May, 1976	20
4. Composition of the species and sex of the carabids caught in the ground and aerial Malaise traps in the Branch Mature and Branch Pole plots northwest of Baldwin in the Manistee National Forest, 1976, 1977	23
5. Summary of all carabids caught on sticky board traps, 1976, in the area of the Branch Mature and Branch Pole plots within the Manistee National Forest northwest of Baldwin, Michigan .	23
6. Summary of all carabids caught on sticky board traps, 1977, in the Branch Mature and Branch Pole plots near Baldwin and 2 at Dublin, Michigan. All traps are within the Manistee National Forest	23
7. Lebiine carabids collected with <u>Pinacodera platicollis</u> and <u>P. limbata</u> in the Manistee National Forest near Baldwin, Michigan, 1976, 1977	34

TABLE

PAGE

2.1	The basal area and density of trees in the Branch Mature and Branch Pole plot areas within the Manistee National Forest near Baldwin, Michigan, 1977	44
2.2	The percentage of basal area of the dominant oak species within the plot areas of Branch Mature and Branch Pole within the Manistee National Forest near Baldwin, Michigan, 1977	44
2.3	Plant species found within the Branch Mature and Branch Pole plots in the Manistee National Forest near Baldwin, Michigan, 1977. These plants are common to both plots though in varying numbers.	44
3.1	Soil characteristics of Branch Mature and Branch Pole plots in the oak-dominated Manistee National Forest northwest of Baldwin, Michigan, 1977	45

LIST OF FIGURES

FIGURE	PAGE
1. <u>Pinacodera limbata</u>	4
2. Location of the research plots within the Manistee National Forest, Baldwin, Michigan, 1976, 1977	6
3. Tree number 1 with sticky board traps at Branch Mature, Manistee National Forest near Baldwin, Michigan, 1976	8
4. An individual board (4 vanes) as used in 1976 in the Manistee National Forest near Baldwin, Michigan	8
5. Placement of sticky board traps, 1976, 1977, in their relationship to the Branch Pole and Branch Mature plots in the Manistee National Forest near Baldwin, Michigan	10
6. A graphic representation of the differences of the ecdysial sutures of the arboreal carabid larvae, presumably <u>Dromius piceus</u> ; a) either a second or third instar, b) first instar with egg bursters. These larvae were collected from white and red oaks in the Manistee National Forest near Baldwin, Michigan, 1975, 1976	17
7. Comparison of sticky board trap trees with and without adjacent clearings from 1976 and 1977 in the Manistee National Forest near Baldwin, Michigan	25
8. The weekly catch of <u>Pinacodera limbata</u> from the blacklight trap in the Manistee National Forest southwest of Baldwin, Michigan, 1976	26
9. The weekly catch of <u>Pinacodera limbata</u> , males and females, from the blacklight trap at Big Star Lake southwest of Baldwin, Michigan, in the Manistee National Forest, 1977	27
10. The weekly catch of <u>Dromius piceus</u> from the blacklight trap at Big Star Lake southwest of Baldwin, in the Manistee National Forest, Michigan, 1977	28
11. The catch of male and female <u>Pinacodera platicollis</u> from glycol-filled pitfalls of the Branch Mature and Branch Pole plots, Manistee National Forest near Baldwin, Michigan, 1977	29

12. The catch of male and female <u>Pinacodera limbata</u> from glycol-filled pitfalls of the Branch Mature and Branch Pole plots, Manistee National Forest near Baldwin, Michigan, 1977	30
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INTRODUCTION

The Carabidae is one of the largest and most commonly collected beetle families. The common name, ground beetles, reflects the concept of carabids as insects that spend much of their time in close association with the soil. This is true for a majority of carabid species; however, many species are arboreal or planticolous, climbing on plants. Most of these arboreal species belong to the tribe Lebiini.

Within the Lebiini, many species have atypical life cycles. For example, species of Lebia, the largest genus, are ectoparasitoids of Chrysomelid pupae (Lindroth 1969), a mode of existence found in very few other carabids. Overall, however, the Lebiini may be the least known biologically of the carabid tribes.

Pinacodera, a genus endemic to North America, is one group in the Lebiini whose biology is not well documented. Most of the known biological information relates to the habitat where adults have been collected (Blatchley 1910, Lindroth 1954). The taxonomy of the group also needs work (Horn 1881, 1882, Casey 1920, Lindroth 1969). Of the 23 described species, several are likely to be synonyms, while more species may yet be described (Ball, personal communication).

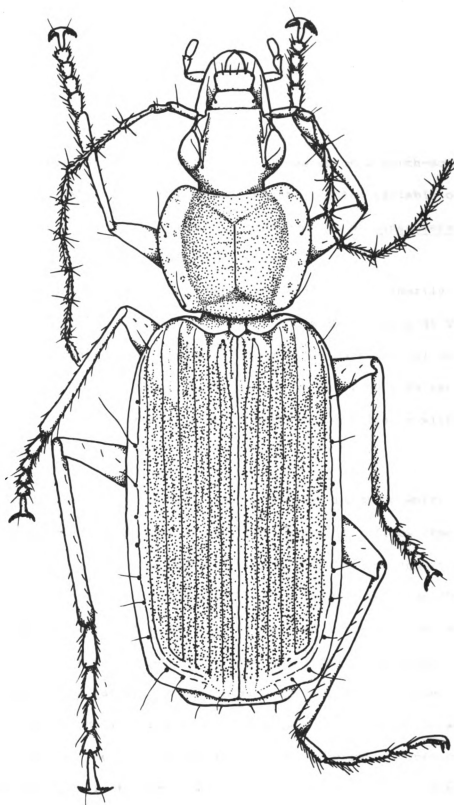
Members of the genus range from Nova Scotia to Ontario, south to Florida and California and into Mexico and Guatemala. The greatest concentration of species is in the American southwest and Mexico (Erwin, et al. 1977). Only 6 species are found east of the Mississippi River and of these, 2 are common, Pinacodera limbata Dejean and P. platicollis

Say (Erwin, et al. 1977). In Michigan, as far as known, these 2 species have been found in the Lower Peninsula only (Hubbard and Swartz 1878). A brief description of both species is given in the appendix.

While studying the variable oak-leaf caterpillar in western Lower Michigan, Wallner and Surgeoner found large numbers of P. limbata (Figure 1) and P. platicollis adults in spray samples from oak trees (personal communication). cursory examination of the literature revealed little biological information other than the attraction of P. limbata to sugar baits (Lindroth 1954).

Because of these large numbers and their presumed impact within the ecosystem, a study of the Pinacodera species in the Baldwin, Lake County, area of the Manistee National Forest was initiated. The objectives of the study were: 1) determine the life cycles of both species; 2) determine their seasonal appearance and 3) associate larvae with adults.

Figure 1. Pinacodera limbata



METHODS

Plots and plot conditions

Plots: Surgeoner (1975) used 5 plots situated on a north-south axis through the MNF (Manistee National Forest) for the variable oakleaf caterpillar study. Two exhibiting high humbers of Pinacodera adults were chosen for the carabid study (Figure 2).

While generally similar, the 2 plots differed primarily in the age class of trees. Branch Pole (referred to as BP, located at T18N R14W sec. 5) was characterized by pole-sized trees on a gradual south-west facing slope; Branch Mature (referred to as BM, T18N R14W sec. 4) was characterized by mature trees on a north-facing hillside with alternating ridges and ravines.

Plot Conditions: In the late 1800's, a mixed hardwood-white pine forest was logged off in the area of the MNF. Subsequent fires removed both slash and soil nutrients making the soil too poor to support agriculture. As a result, a predominantly oak forest reclaimed the land (Dunbar 1955). In the upland areas, the dominant trees, red and white oak, are found associated with bigtooth aspen Populus grandidentata Michaux, jack pine, Pinus banksiana Lambert and red maple, Acer rubrum Linnaeus.

Acidic sandy loam soil covers most areas of the MNF as well as the plots. Within the plots a layer of leaves of varying depth covers a 6 to 8 cm thick root zone. Despite the layer of litter, both soil and litter rapidly dry after precipitation. See the appendix for further information on stand composition and density in the plots as well as soil characteristics.

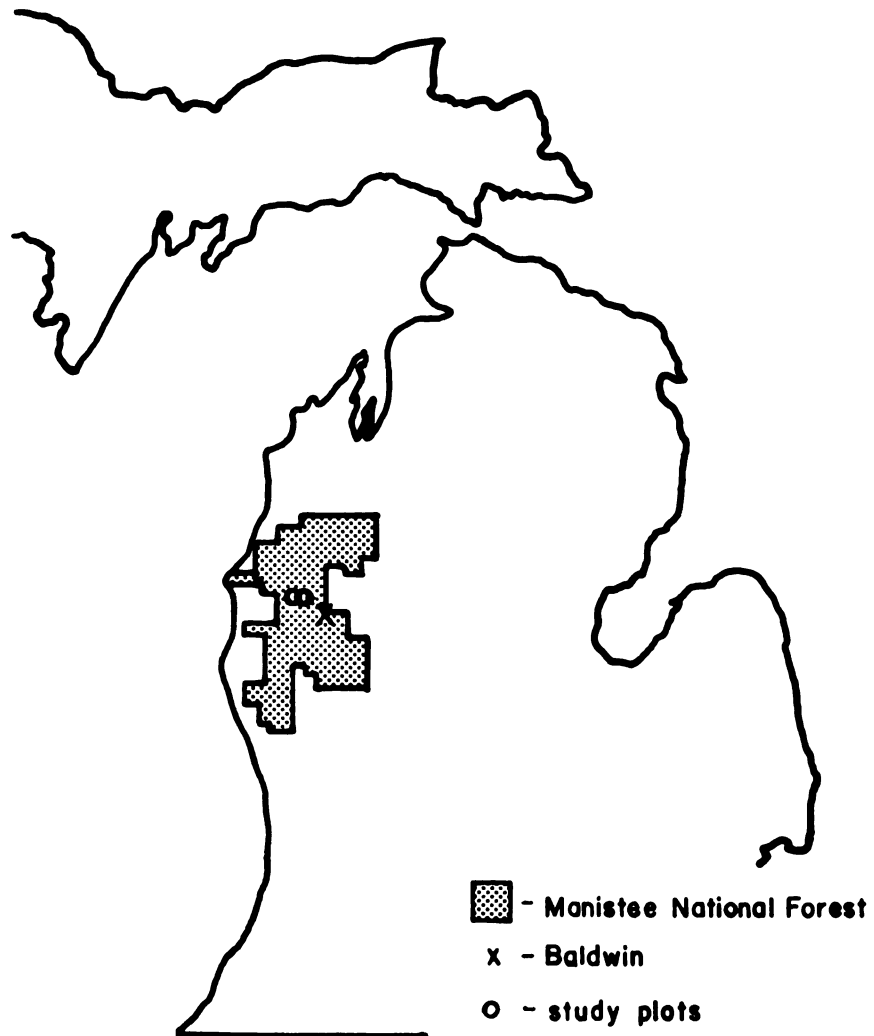


Figure 2. Location of the research plots within the Manistee National Forest, Michigan, 1976, 1977.

Trapping methods

Nine major collecting methods were employed over the 2 year study. For convenience, these methods have been divided into 2 groups: fixed traps and movable traps.

Fixed Traps

Malaise traps: Two directional Malaise traps of the Towne's design were utilized for detecting the presence of Pinacodera adults. In addition to sampling carabids, they provided useful information regarding the insect fauna of the plots. Two levels were sampled: ground level and the 10 m height.

One ground Malaise was placed at BP and 1 aerial Malaise was erected at BM. Both were maintained for the 2 years from mid-May to mid-September. The traps were checked on a weekly basis, except the 1977 aerial Malaise which was checked biweekly.

Sticky Boards: Eye hooks screwed into tree limbs at the 10 m height supported a clothesline rope to which sticky boards were either stapled or tied (Figure 3). The boards were hung at 3 levels, 1.5, 5 and 8.5 m.

The 1976 traps were constructed of Zoecon^(R) codling moth sticky boards stapled back to back forming a cross, with a rope running through the center (Figure 4). In 1977, to reduce costs, $\frac{1}{4}$ " plywood panels, slotted in the center, replaced the Zoecon^(R) boards. The panels were soaked in linseed oil to prevent warping and dehydrating the Tack Trap^(R) applied to the surfaces. The boards were later touched-up with Aerosol Tanglefoot^(R). The surface area for 1 unit of sticky board was .3 sq. m.

A total of 14 trees, including both red and white oaks, were used to support traps. These trees were chosen for their accessibility and conformation. In 1976, 8 ropes were set by July 1 and used until September 23.



Figure 3. Tree number 1 with sticky board traps at Branch Mature, Manistee National Forest near Baldwin, Michigan, 1976.



Figure 4. An individual board (4 vanes) as used in 1976 in the Manistee National Forest near Baldwin, Michigan.

In 1977, 6 traps were set, 4 within the plots and 2 at Dublin, Michigan (Figure 5). The 1976 traps were checked at irregular intervals while the 1977 traps were checked weekly.

An index was devised to explain differences in the trap catches between trees. The main factor for the index was the presence or absence of a small clearing adjacent to the trap trees.

Both parametric and non-parametric statistical tests were conducted on the sticky board results. Non-parametric tests involved Chi-square and the Kruskal-Wallis test for inter-group differences (Zar 1974). A t-test was performed on the numbers of carabids caught per sticky board trap tree.

Pitfall Traps: Fifteen unbaited pitfall traps made from soda pop cans were set in each plot in 1976 and used from mid-July to mid-September.

The number and design of pitfall traps changed in 1977. Cottage cheese containers, 0.53 liter (1 pint) capacity, were filled with 2-3 cm with ethylene glycol. Plywood or masonite covers prevented rain and excessive litter from entering the traps. Plywood covers were soaked in linseed oil to prevent warping.

Twenty of these traps were set in 2 series of 10 in each plot. The series were set perpendicular to each other, 20 m apart. Inter-trap spacing was 10 m.

In mid-July, 1977, an additional 60 traps, uncovered and empty, were set. In each plot, 30 traps were set in 3 series of 10 with a 5 m spacing between traps. These traps were widely separated from the glycol-filled traps to prevent biased results, but otherwise were positioned to sample as much diversity of habitat as possible. The uncovered traps were checked at least every fourth day.

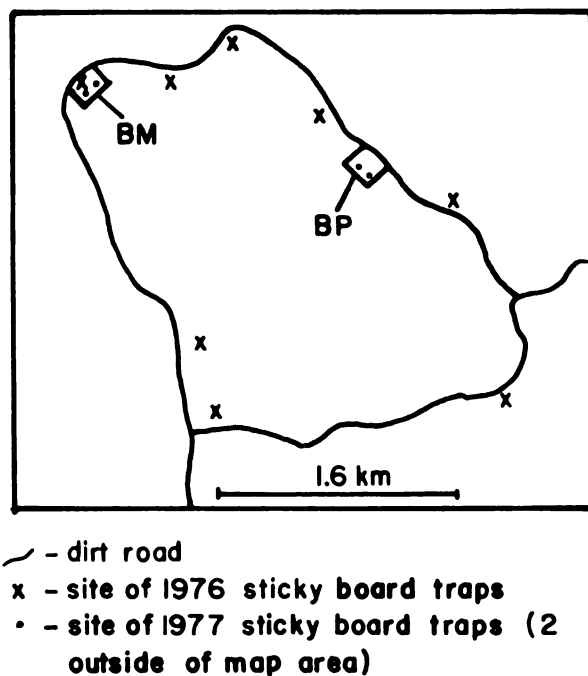


Figure 5. Placement of sticky board traps, 1976, 1977, in their relationship to the Branch Pole and Branch Mature plots in the Manistee National Forest near Baldwin, Michigan.

Blacklight: A blacklight trap was run outside of the plots both years in an area comparable to BP. Approximately 114 gm of Cyanogas^(R) were used and changed weekly when the trap was checked. Trapping began in late May and was terminated by mid-October. Multiple linear regression was used to correlate temperature, humidity and the number of P. limbata in both years.

Winter Soil Sampling: A 30 m square plot was marked off in a wooded area 9.5 km east of the BP plot. From here, soil samples of 15 x 15 x 15 cm were taken randomly. Twenty samples were collected biweekly during the 1976 and 1977 winters and removed to the laboratory where they were subjected to Berlese funnels. A total of 160 samples were processed.

Movable trapping

Pyrethrum Spraying: Using a ladder truck and a back pack mist blower, trees up to 15 m tall were sprayed. The criteria for spraying were accessibility with the ladder truck and proper height. Four and one half liters of spray solution containing .141 of 0.5% (AI) of pyrethrum was sufficient for good coverage of most trees (Surgeoner 1975). A nylon tarp was spread beneath the tree before spraying. After most of the insects had fallen (approximately 15 minutes after spraying), they were gathered and preserved in 90% ethyl alcohol. On the average, one red and one white oak were sprayed each week during the summer of 1976. In 1977, only 4 trees were sprayed.

Night Collecting: Head-mounted flashlights were used to scan the tree trunks for adult carabids shortly after dark. Adults were taken back to the laboratory for identification and sex determination. In 1977, several different localities were visited to ascertain the presence of the Pinacodera species. Stand and weather conditions were recorded and

collecting was done for $\frac{1}{2}$ hour at each site.

Bark Stripping: This method determined if adult Pinacodera were present on white oaks during daylight hours. Only white oaks were involved since they have large exfoliating bark scales which provide hiding places for insects and other arthropods. Usually the main trunk was debarked, the total distance dependent upon the conformation of the tree and time available.

Hand Collecting: Hand collecting involved digging through leaf litter at the tree base to find adult beetles during the spring and fall. Beginning in May of 1976, 5 weekly transects were made in each plot. The transects were 100 paces, straight lines perpendicular to a standard baseline. Each baseline was 200 m long with 200 points, 1 m apart. The point of origin for each transect was determined randomly. Trees encountered on or within $\frac{1}{2}$ pace of the transect were examined around the base for adult Pinacodera.

Biology investigations

Feeding Trials: For feeding trials, 1 liter, waxed containers with screen lids were used. A pair of P. platicollis adults was placed in each. Sand, leaves and small twigs served as substrates. A total of 17 pairs of adults was kept for 27 days. Soft bodied insects, such as caterpillars and beetle larvae, were offered every other day. The number and stage of development of the prey (if known) was recorded. Small wads of tissue, kept moist, provided a source of water.

Rearing Experiments: Rearing containers were 0.53 liter plastic cottage cheese containers with clear plastic lids. Dampened peat moss, which retarded the growth of mold, was used as a substrate. Ten adults could

be placed in such a container with 2 cm of peat moss without cannibalism. The peat moss was checked every other day for larvae. Small chunks of apple dipped in a water solution of casein hydrolysate served as food.

Winter Cage: In an attempt to discern the overwintering sites of adult *Pinacodera*, 35 *P. platicollis* and 5 *P. limbata* were released within a floorless 2 x 2 x 2 m nylon cage during late October, 1976. The floorless condition allowed the beetles full movement in the leaf litter within the confines of the cage. Aside from shallow trenches dug to bury the cage flaps, which prevented movement in or out of the cage, the natural cover was not disturbed. An area with a high diversity of ground cover was chosen, including a 10 cm white oak. In late November, the cage was removed to facilitate sampling. Aluminum yard skirting replaced the cage flaps to prevent insect movement within the litter.

Beginning in late December, 1976, 20 soil samples, 15 x 15 x 15 cm were removed, biweekly, in a systematic manner from the cage. These were returned to the laboratory and subjected to Berlese funnels.

Dispersal Experiment: This experiment was devised to determine how quickly carabids reinvaded sprayed trees and whether or not flight was involved. In early August of 1976, 4 pairs of trees, including both red and white oaks, were physically separated from surrounding trees by pruning and were sprayed with pyrethrum in the normal dosage. Immediately after spraying, one tree of each pair was banded with a 15 cm wide band of Tack Trap^(R). The 4 pairs were resprayed 1 day later, 2 days later, 6 days later and 8 days later, respectively.

Dissection of Females: Females of both species were examined to determine the age of the female and the number and stage of development of eggs. If

yellow bodies (corpea lutea) were found in the ovarioles or if the ovaries had atrophied, the females had probably laid eggs (Anderson, personal communication).

Larval rearing: Once larvae were recovered either from the field or from containerized adults, they were reared in glass jars (80 ml) with screw caps and filled $\frac{1}{4}$ full with moistened sphagnum moss. Larvae were given live Tribolium confusum larvae at a rate of 4-5 every 3 days. Diapausing carabid larvae were placed in an GCA^(R) environmental chamber which was set for 5°C. After 12 weeks, the temperature was gradually increased to 17°C over a period of 30 days.

Temperature recording

Weather data, including high and low temperatures, humidities and rainfall were obtained from the United States Forest Service at the Baldwin District Office in Baldwin.

Soil testing

Three soil samples were taken from each plot and tested for pH, composition by particle size and percent organic matter. The analysis was completed by the Soils Testing Laboratory, Michigan State University. The findings are presented in the appendix.

RESULTS

Data Prior to September, 1975

Information from Surgeoner's study (1975) of the variable oakleaf caterpillar indicated the presence of 3 tree dwelling carabid species, Pinacodera platicollis Say, P. limbata Dejean and Dromius piceus Dejean. Both carabid adults and larvae were removed from pyrethrum spray and Malaise trap samples of that study. The larvae were identified as lebiine larvae using Emden's larval key (1942).

A total of 22 larvae represented 2 different instars, indicated by the differences in the shape of the ecdysial sutures and presence of egg bursters in the small form. Those larvae with egg bursters, first instars, had "U"-shaped ecdysial sutures compared to the "Y"-shaped ecdysial sutures of the later instars (Figure 6). Initially, it was felt that the larger instars were Pinacodera larvae.

Pyrethrum Spray Results - 1976

Two hundred adult Pinacodera and 44 adult Dromius were recovered from 32 spray samples (Table 1). Five larvae were collected, 3 by spraying and 2 by other means. Although Pinacodera adults were most numerous in the trees in late spring and mid-summer, P. platicollis was in the trees in April and May before the oaks had leafed out. Dromius piceus was found in all areas where Pinacodera were collected but favored trees in dry, grassy areas.

Bark Stripping - 1976, 1977

Stripping of bark scales of 10 white oaks indicated that probably adults of both genera were confined to the trunks and larger limbs.

Figure 6. A graphic representation of the differences of the ecydsial sutures of the arboreal carabid larvae, presumably Dromius piceus; a) either a second or third instar, b) first instar with egg bursters. These larvae were collected from white and red oaks in the Manistee National Forest near Baldwin, Michigan, 1975, 1976.

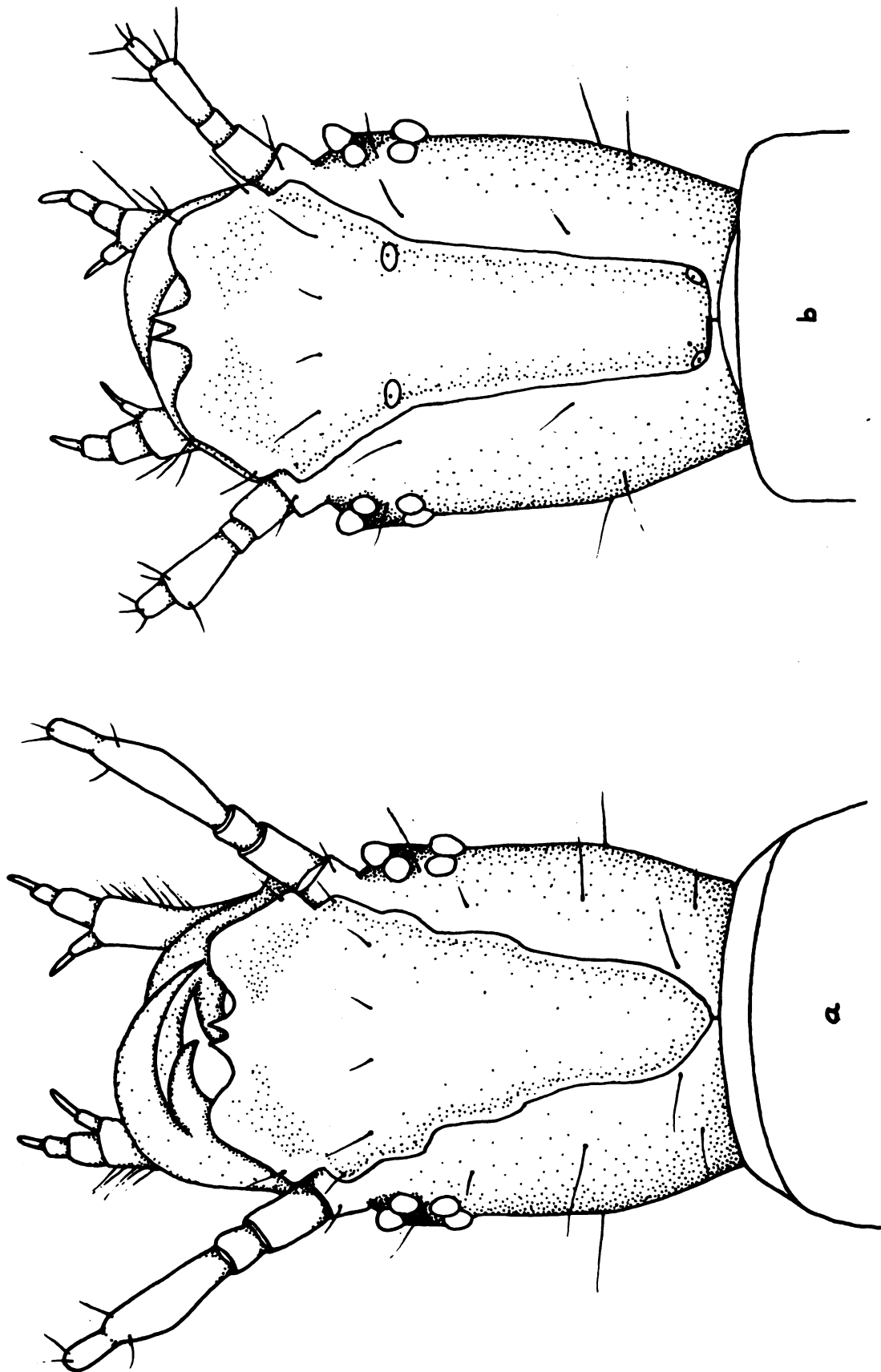


Table 1. Means of Pinacodera platicollis, P. limbata and Dromius piceus taken from spray samples from red and white oaks in the Manistee National Forest around Baldwin, Michigan, 1976.

	Red Oak	White Oak
# of trees sprayed	12	20
total # of <u>P. platicollis</u>	15	101
mean # per tree	1.25	5.05
total # of <u>P. limbata</u>	26	66
mean # per tree	2.16	3.30
total # of <u>D. piceus</u>	27	18
mean # per tree	2.25	.90

Table 2. The number of Pinacodera limbata recovered from the second spraying of four pairs of trees near the Branch Pole plot in the Manistee National Forest northwest of Baldwin, Michigan, August, 1976.

	Pair 1	Pair 2	Pair 3	Pair 4
Banded	0	1	2	3
Unbanded	0	0	5	2

From 1-17 adult Pinacodera and 0-3 Dromius adults were found per tree, always more than 2 m high on the trunk.

Only one immature form, a pupa, was collected August 31, 1976, using this method. The pupa, a cream-white color, except for the darkened eyes and mandibles, hung upside-down with its dorsum towards the trunk. Long hairs kept it clear of the bark. The following day it emerged and was identified as D. piceus.

Dispersal Experiment - 1976

Results of the dispersal experiment indicate that there is flight activity between trees of P. limbata (Table 2). On the sixth and eighth days, the number of P. limbata recovered was comparable to trees sprayed only once.

Hand Collecting - 1976

Results of the 5 transects made in the plots showed that the ground-dwelling adults of P. platicollis were associated with only 25% of the trees within the plots. The majority of the trees of this 25% were red oaks (Table 3). Only 5 P. limbata were collected.

Both transects and general hand collection in the litter indicated that P. platicollis was common in the spring, with up to 14 adults being collected about a single tree. Adults of P. limbata were more scarce with never more than 2 adults being found around one tree. Only an occasional D. piceus adult was collected.

By late June, P. platicollis could not be found but P. limbata was present at a rate of less than 1 adult per tree. From mid-July to early September, very few adults of either species could be collected around any tree. By mid-September, however, numbers of Pinacodera increased but did not reach spring levels.

Table 3. The ground population of Pinacodera platycollis as determined from five weekly transects made in the Branch Mature and Branch plots in the Manistee National Forest, Baldwin, Michigan, April and May, 1976.

Tree Species	Total # of trees sampled	BP		BM	
		Total of <u>P. platycollis</u>	# <u>P. platycollis</u> per tree	Total of <u>P. platycollis</u>	# <u>P. platycollis</u> per tree
Red Oak	15	32	2.13	17	1.12
White Oak	28	11	.39	5	.20
Other	14	3	.21	11	.18

Soil Sampling - 1976, 1977, 1978

Adult Pinacodera removed from soil samples of the winter cage indicated that both species are probably able to overwinter in the leaf litter. However, soil samples taken from BP in January, 1976, and 1978, and samples from the 30 m square in 1977, did not produce any Pinacodera adults or larvae. Instead, several specimens of Dromius piceus and Cymindis neglecta Haldeman were found in the BP samples and several adults of Metabletus americanus Dejean were recovered from the 30 m square.

Night Collecting - 1976, 1977

Adults of both Pinacodera species would climb the tree trunks at dusk after light intensities were less than 1 foot-candle. Peak climbing activity lasted for about 90 minutes in which time the carabids moved quickly up the tree trunks. A period of 10 minutes was ample for any given adult to climb into the canopy. When in the beam of a flashlight, a beetle's typical reaction was to stop and drop or move quickly to a dark area of the trunk and continue climbing. Despite these reactions to a flashlight beam, it was not uncommon to collect 15-20 adults in an hour. Carabids were collected from all tree species within the plots including dead trees. As at dusk, a similar movement down the tree was observed shortly before sunrise. Other species taken from the trunks at night included 10+ Dromius piceus and 1 Calosoma calidum Fabricius.

In both years, the catch of P. limbata at night was strongly male oriented. For 4 recorded observations in 1976, the male:female ratio was 33:11 and for 16 observations in 1977, the male:female ratio was 86:40.

P. platicollis was recorded in night collecting only for late summer

and fall, since spring collection was not possible. The male:female ratio of P. platicollis favored females more than P. limbata being 17:16 in 1976 and 6:17 in 1977.

Malaise Traps - 1976, 1977

P. limbata was the primary carabid collected in both the ground and aerial Malaise traps. The ground Malaise at BP collected 13 adults taken from samples from May 13 to September 1, 1976. The aerial Malaise had 10 adults, from samples taken from June 17 to August 24, 1976. One male P. platicollis and 2 specimens of a Pterostichine carabid, Calathus gregarius Say were also collected in the aerial trap. A total of 12 P. limbata and 2 C. gregarius were taken from the ground Malaise and 17 P. limbata and 3 female P. platicollis were taken from the aerial trap for 1977 (Table 4).

Sticky Board Traps - 1976, 1977

In 1976, 5 species of carabids were collected from the 8 sets of sticky board traps (Table 5). Plochionus timidus Haldeman was not collected by any other method. Episcopellus autumnalis Say, a harpaline carabid, signaled a very localized population, later determined by pit-falls (Liebherr and Mahar 1978).

Only the 3 principal species of P. platicollis, P. limbata and D. piceus were collected in 1977 even though the 6 sets of traps were out 3 months longer than the traps in 1976 (Table 6).

For both years it is evident that the catch of P. limbata was stratified, i.e., the higher the trap level, the greater the numbers of P. limbata caught, which was statistically significant ($P \leq .005$). In addition, the flight activity of P. limbata, as reflected by the overall catch, was consistent for both years ($P \leq .01$). Regression

Table 4. Composition of the species and sex of the carabids caught in the ground and aerial Malaise traps in the Branch Mature and Branch Pole plots northwest of Baldwin, Michigan, in the Manistee National Forest, 1976, 1977.

Year		Ground		Aerial	
1976	Species	♂	♀	♂	♀
	<i>Pinacodera limbata</i>	4	9	5	5
	<i>P. platicollis</i>	1	0	0	0
	<i>Calathus gregarius</i>	1	1	0	0
1977					
	<i>Pinacodera limbata</i>	5	7	6	13
	<i>P. platicollis</i>	0	0	0	3
	<i>Calathus gregarius</i>	1	1	0	0

Table 5. Summary of all carabids caught on sticky board traps, 1976, in the area of the Branch Mature and Branch Pole plots within the Manistee National Forest northwest of Baldwin, Michigan.

Species	Level (m)		
	1.5	5	8.5
<i>Pinacodera limbata</i>	10	29	53
<i>Pinacodera platicollis</i>	2	1	8
<i>Dromius piceus</i>	3	2	5
<i>Plochionus timidus</i>	0	2	4
<i>Episcopellus autumnalis</i>	1	0	0

Table 6. Summary of all carabids caught on sticky board traps, 1977, in the Branch Mature and Branch Pole plots near Baldwin, and 2 at Dublin, Michigan. All traps are within the Manistee National Forest.

Species	Level (m)		
	1.5	5	8.5
<i>Pinacodera limbata</i>	6	9	23
<i>Pinacodera platicollis</i>	0	0	2
<i>Dromius piceus</i>	6	2	3

analysis on 1977 sticky board data with high temperatures and humidity shows a correlation of $R^2=0.597$.

The results of the index of the trap trees are represented in Figure 7. Those trees with adjacent small clearings had a significantly greater catch of P. limbata than those trees without clearings or adjacent to clearcut areas ($P \leq .01$).

Blacklight - 1976, 1977

As in the Malaise traps, P. limbata was the primary carabid collected. Only 2 P. platicollis were taken in the 2 years of the study. In both 1976 and 1977, peak periods occurred in July (Figures 8, 9). As with night collecting, the overall catch was male dominated. Dromius piceus was also common in the weekly samples and showed a peak activity period analogous to P. limbata for 1977 (Figure 10).

Pitfall Traps - 1976, 1977

The first attempt at using pitfall traps in 1976 gave little information on the movement of Pinacodera in the leaf litter. Only 2 P. limbata were collected. In 1977, the glycol-filled traps caught many adults, primarily females of both species (Figures 11, 12). Pinacodera larvae were not collected in these traps.

The empty pitfall traps collected 18 supposed Pinacodera larvae, 17 from BP and one from BM, from July 14 to October 27. Of these, only 1 may have been a third instar, collected on August 4. Other carabid larvae were collected, but not all could be identified (Liebherr and Mahar 1978).

Larval Rearing - 1977, 1978

Six larvae were reared from containerized adults, but most of these died in the first instar. Most larvae, both reared and field collected,

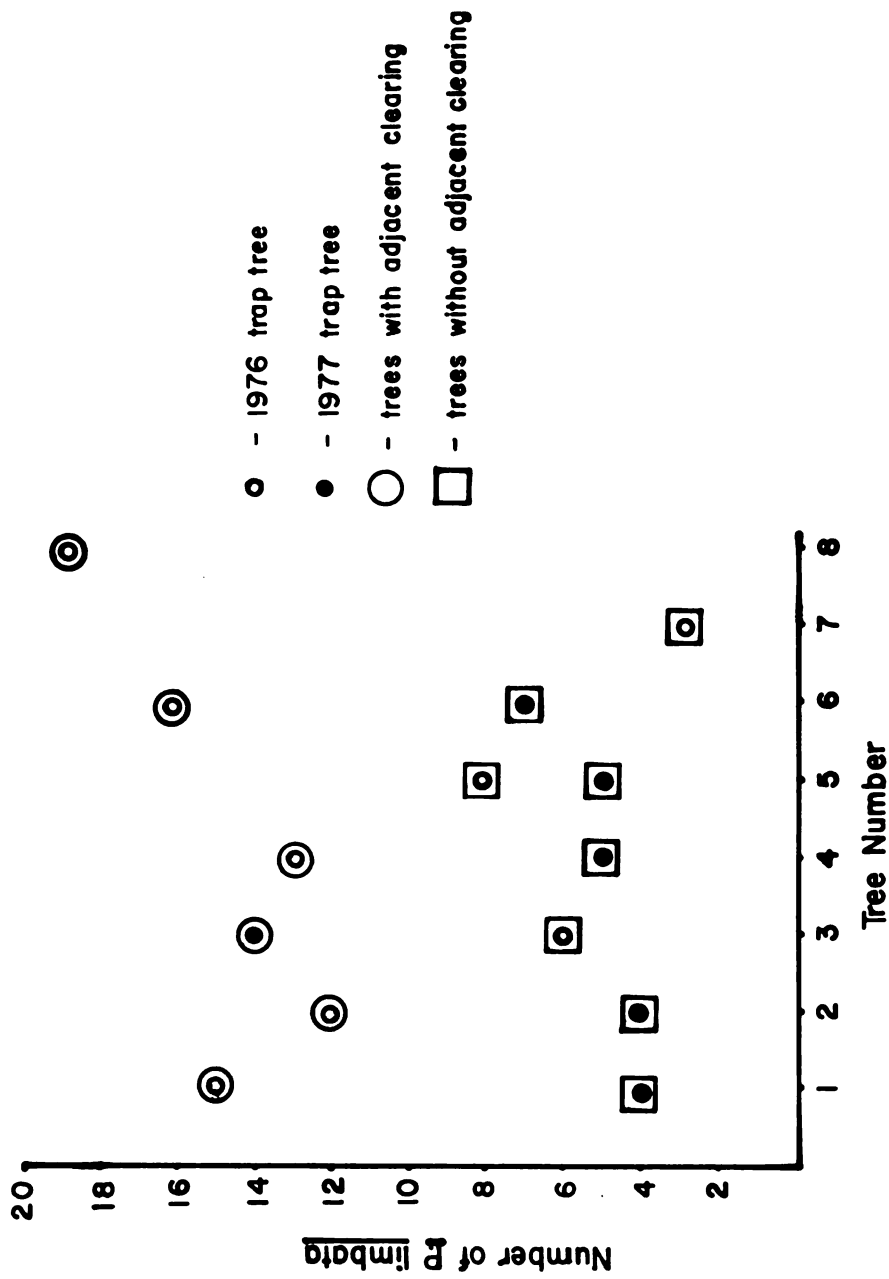


Figure 7. Comparison of sticky board trap trees with and without adjacent clearings from 1976 and 1977 in the Manistee National Forest near Baldwin, Michigan.

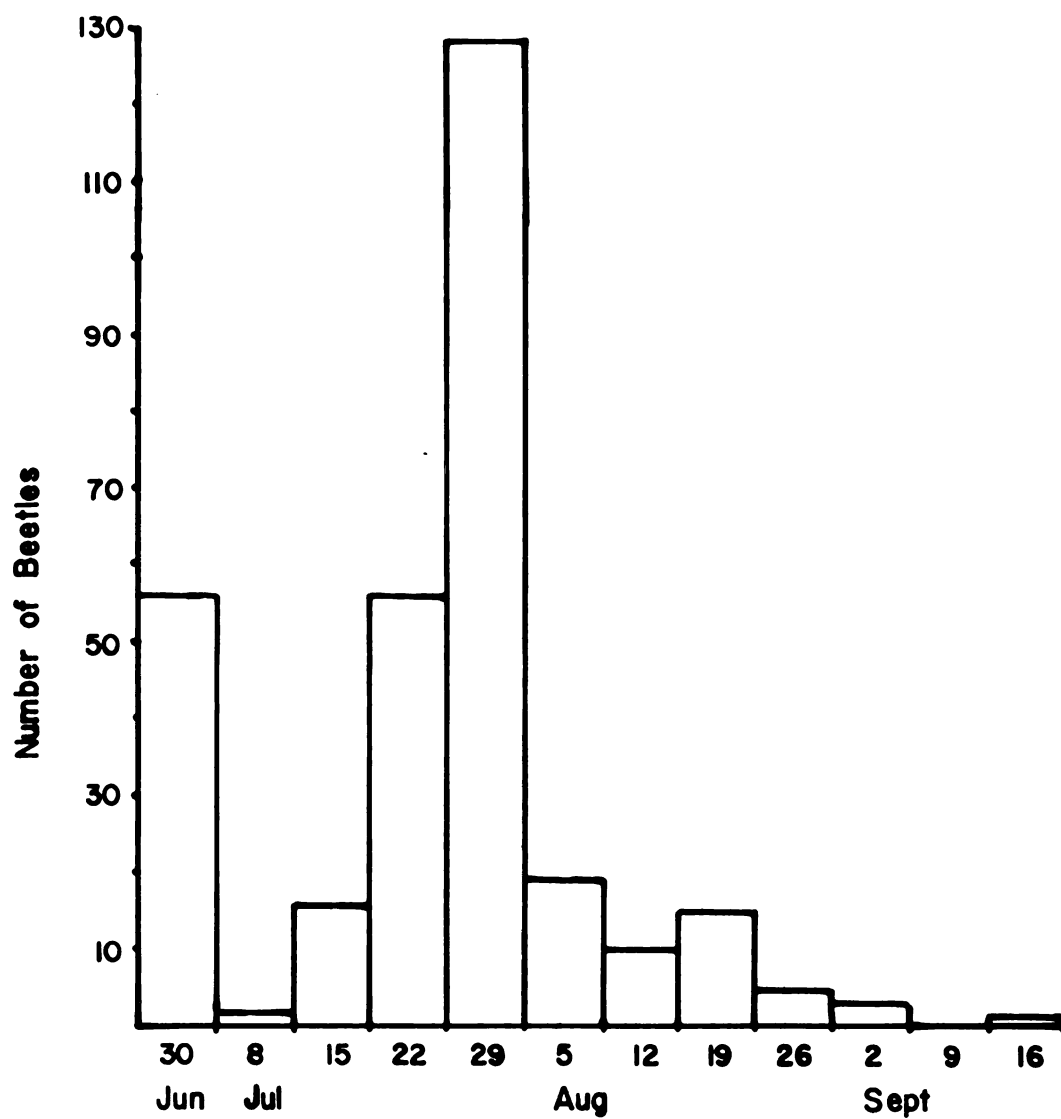


Figure 8. The weekly catch of *Pinacodera limbata* from the blacklight trap in the Manistee National Forest southwest of Baldwin, Michigan, 1976.

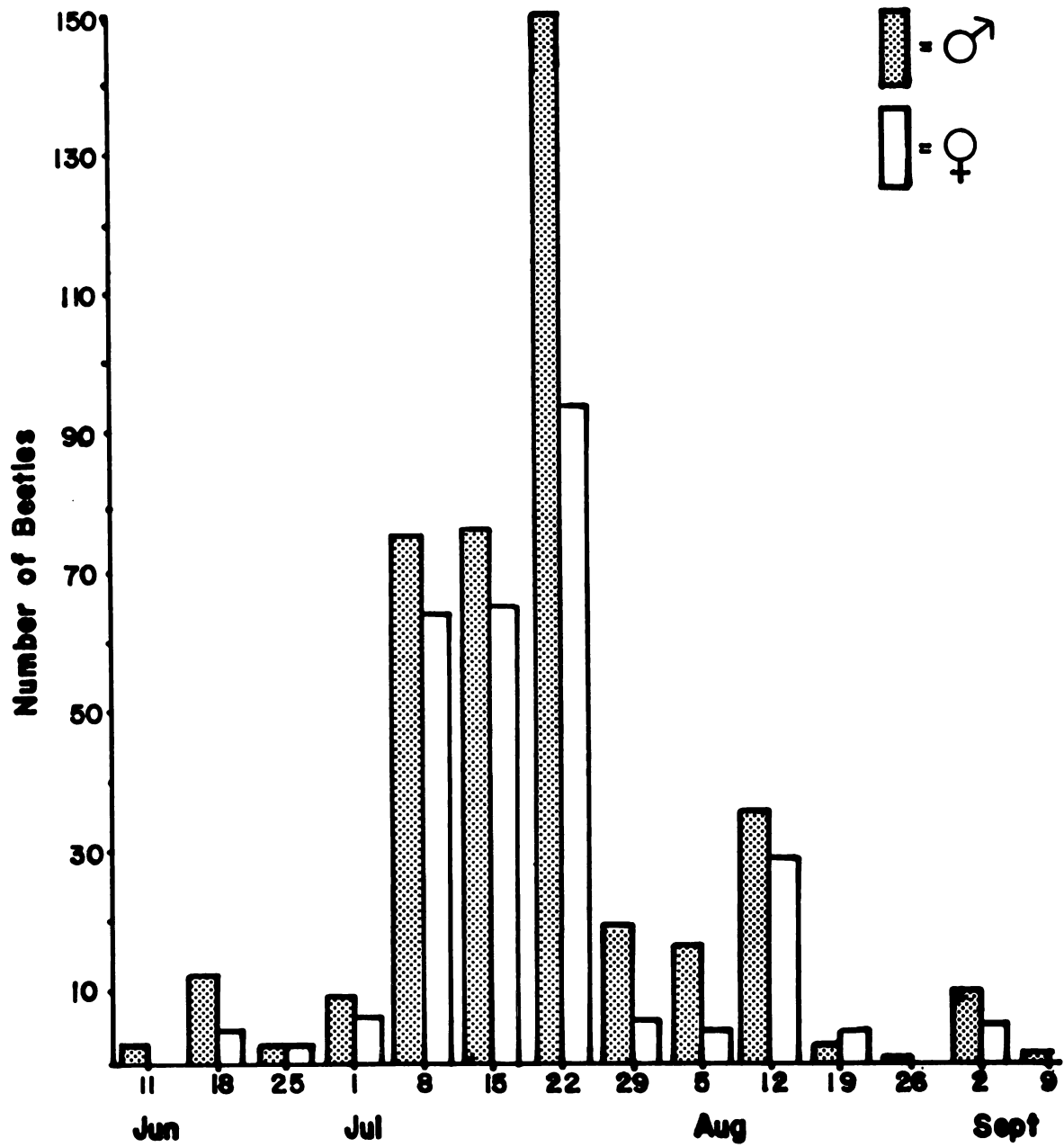


Figure 9. The weekly catch of *Pinacodera limbata*, males and females, from the blacklight trap at Big Star Lake southwest of Baldwin, Michigan, in the Manistee National Forest, 1977.

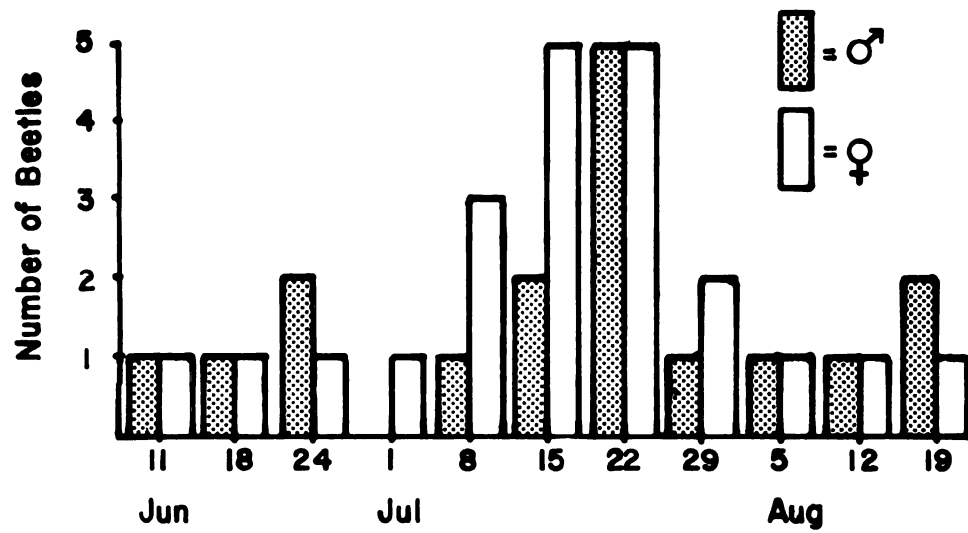


Figure 10. The weekly catch of Dromius piceus from the blacklight trap at Big Star Lake southwest of Baldwin, in the Manistee National Forest, Michigan, 1977.

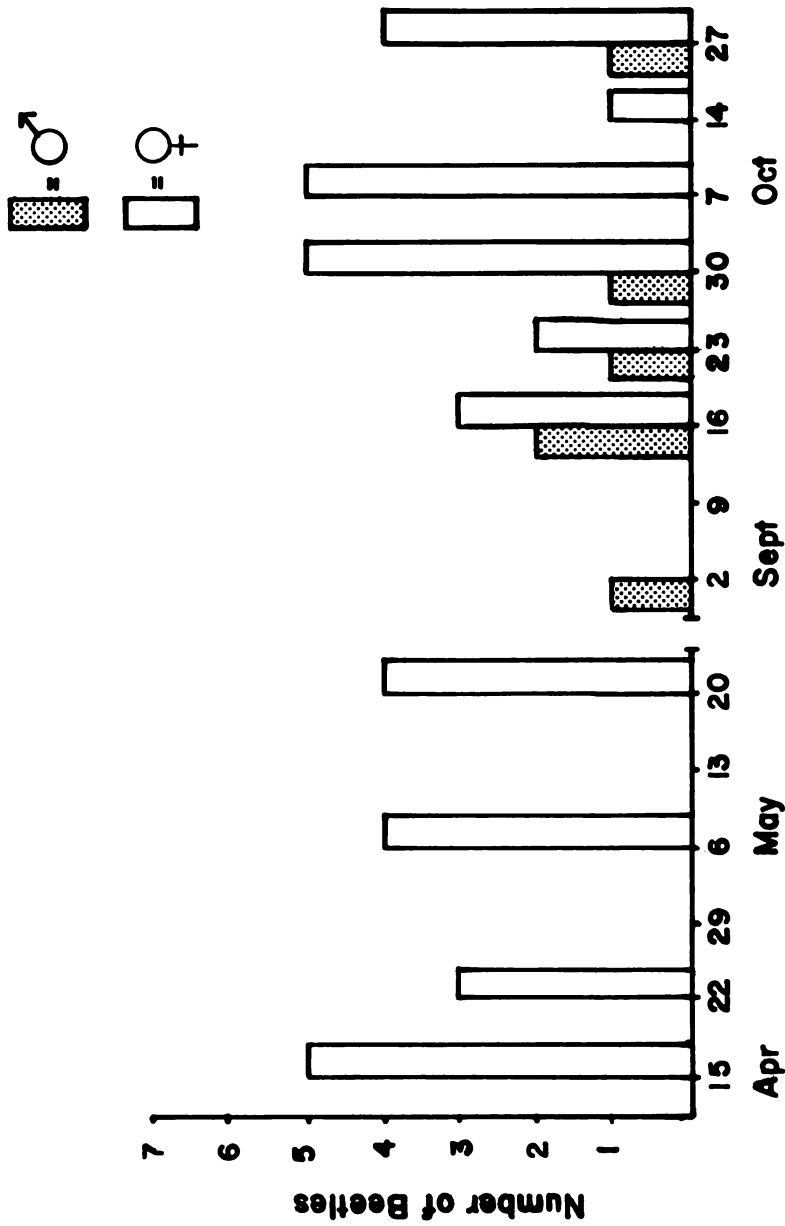


Figure 11. The catch of male and female *Pinacodera platicollis* from glycol-filled pitfalls of the Branch Mature and Branch Pole plots, Manistee National Forest near Baldwin, Michigan, 1977.

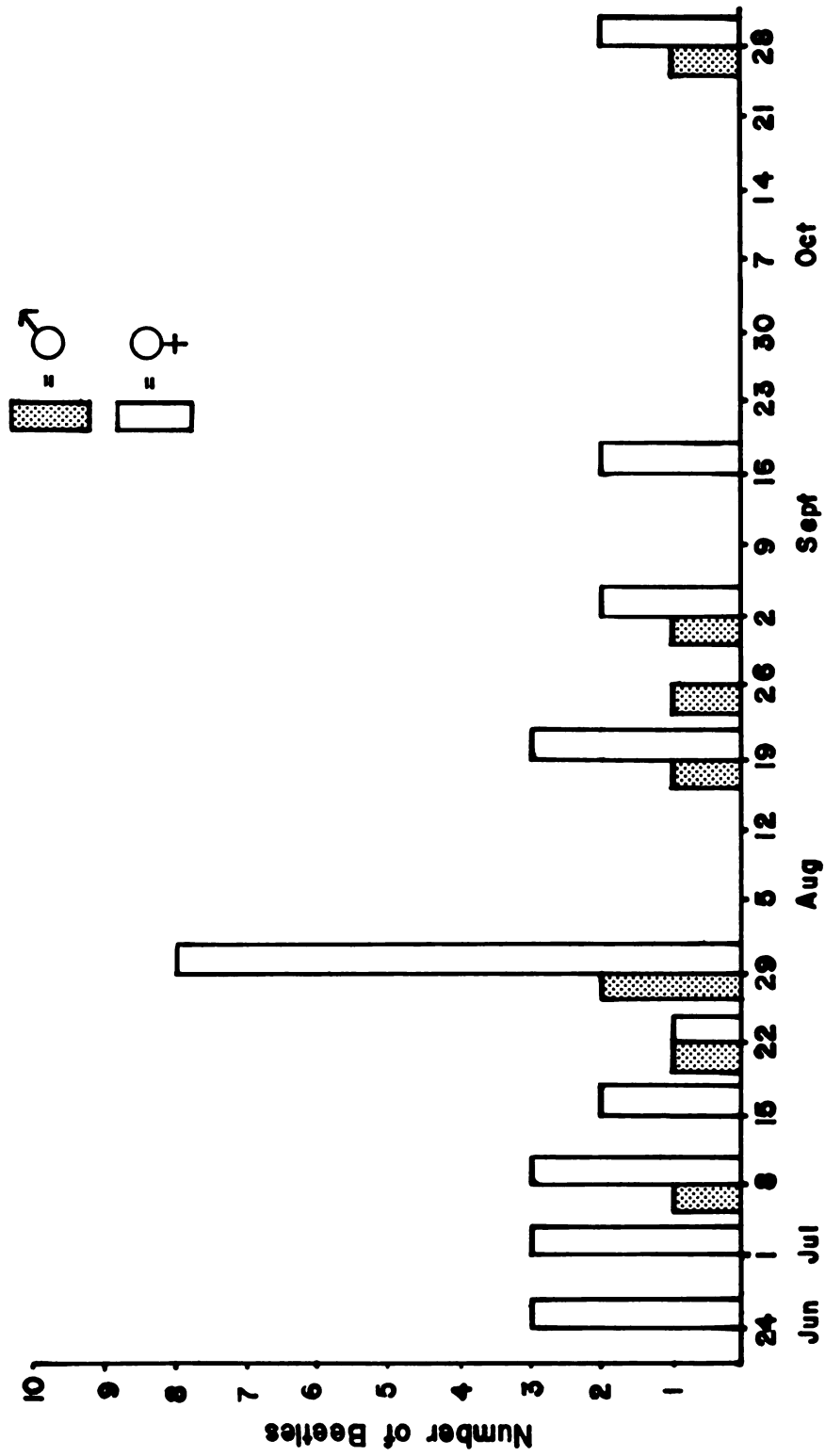


Figure 12. The catch of male and female *Pinacodera limbata* from glycol-filled pitfalls of the Branch Mature and Branch Pole plots, Manistee National Forest near Baldwin, Michigan, 1977.

entered an apparent non-feeding diapause stage by mid-August. Eight larvae, including field specimens and reared specimens, were given a cold treatment in September. Three of these survived to the pupal stage, but only 1 emerged as an adult. It was identified as Cymindis neglecta. Twelve days after pupation the eyes had darkened and 8 days later the adult emerged. Examination of cast skins of this specimen show no obvious differences when compared to the cast skins and larvae of reared Pinacodera larvae.

Feeding Trials - 1976, 1977

Insects that were consumed by laboratory held adults of both species are listed below:

<u>Family</u>	<u>Species</u>	<u>Instar</u>
Notodontidae	<u>Heterocampa manteo</u> (Doubleday)	1st, 2nd
Lasiocampidae	<u>Malacosoma americanum</u> (Fabricius)	1st, 2nd, 3rd
Tortricidae	unknown	unknown
Hesperiidae	unknown	unknown
Tenthredinidae	unknown	unknown
Tenebrionidae	<u>Tribolium confusum</u> Duval	unknown

In general, less pubescent larvae were preferred over more pubescent larvae. Later instars of Heterocampa manteo were not taken, presumably because of the development of a cervical gland capable of ejecting formic acid (Surgeoner 1975).

Dissection of Females - 1976, 1977

Dissection of females of both species showed that each ovary consisted of 6 ovarioles, a common oviduct but no accessory gland. At

most, only 2 supposedly mature eggs were found within any one female. These eggs were gray-white in color, $1\frac{1}{2}$ mm long and 1 mm wide, with isodiametric microsculpture evident. Excised eggs dehydrated quickly and attempts to rear larvae from them did not succeed.

Reproductively mature female P. platicollis were collected in September, October, April and May while reproductively mature P. limbata females have been collected from the third week of June to late August.

Females of P. limbata collected in September and October showed different internal morphological states. Three females caught in September, 1977, had greatly atrophied internal organs, with the ovaries, defensive fluid reservoirs and digestive tract transparent and flaccid. Two females caught in October had internal organs that appeared to be in good condition, not atrophied. None of the 5 had eggs and all had yellow bodies (corpora lutea) in the ovarioles indicating that they had all laid eggs (Anderson, personal communication).

Observed Nocturnal Feeding

Three observations of feeding were made while night collecting. A single adult P. limbata was found feeding on the carcass of a membracid, Ophiderma salamandra, and a Bucculatrix sp. cocoon. The third sighting was of several adults feeding on oozing sap of a red maple.

An examination of the proventriculus of both species shows an armament of 4 lobes covered by rasping teeth. There are no apparent structures for heavy grinding of chitinous or herbaceous material. Small prey was kneaded into a pulpy ball before consumption and in the case of a first instar geometrid larva, the head capsule was not eaten.

Predation

Although large spiders were abundant in the plots (e.g. Thomsidae and Lycosidae), no actual predation was observed in the field. Occasionally, elytra of Pinacodera were found in rotted logs and under bark, but causes of death were unknown.

Adults of both species have 2 large muscular reservoirs of defensive fluids which contain at least formic acid in addition to other compounds (Forsyth 1972). These reservoirs may discourage predation.

Associated Lebiine Carabids - 1976, 1977

As has been noted already, Dromius piceus was one of the major lebiine species encountered in the study. Its overall appearance is similar to the Pinacodera species and when night collecting, it was very difficult to distinguish a specimen of D. piceus from smaller males of either Pinacodera species. Individual specimens are approximately 6-7 mm long and are testaceous to brown in color and without maculation. The head is usually darker. The body, as in the Pinacodera species, is dorso-ventrally flattened. Lindroth (1969) notes that D. piceus may be the only true arboreal carabid in North America. Seven other species representing 4 genera were collected during the 2 year study (Table 7).

Life Cycle of P. platicollis and P. limbata - A Summary

Reproductively mature females of P. platicollis can be found in September and October as well as in the spring in April and May. It is unknown if mating and oviposition of eggs occurs in the fall, but these events do occur in the spring. Once mated, it is likely that

Table 7. Lebiine carabids collected with Pinacodera platycollis and P. limbata in the Manistee National Forest near Baldwin, Michigan, 1975-1977.

Species	Pyrethrum Spraying	Sticky Boards	Night Collecting	Soil Samples	Hand Collecting	Blacklight	Pitfall Traps
<u>Lebia viridis</u> Say	May 20, 77 (1)						
<u>Lebia bivittata</u> Fabricius					Oct 23, 77 (1)		
<u>Dromius piceus</u> Dejean	May 27 - Sept 24, 76 (44)	Jul 1-13, 76 (10) May 14-Aug 20, 77 (11)	Jun 30, 77 (1) Jul 2, 77 (2) Aug 22, 77 (1) Sept 2, 77 (2)	Dec, 75 - Jan, 76 (6)		Jun 11 - Aug 19, 77 (39)	
<u>Metabletus americanus</u> Dejean				Jan, 77 - Mar, 77 (8)			May 6, 77 (1) Jun 10, 77 (2) Jun 17, 77 (2) Jul 1 (1) & Jul 8, 77 (1)
<u>Plochionus timidus</u> Haldeman		Jul 10, 76 (2) Jul 27, 76 (1) Sept 8, 76 (2)					
<u>Cymindis neglecta</u> Haldeman				Dec, 75 - Jan, 76 (3)			Aug 22, 77 (1 larvae)
<u>Cymindis pilosa</u> Say						Jul 1-8, 77 (5)	
<u>Cymindis craticollis</u> Dejean					Aug 7, 77 (1) Aug 17, 77 (1)		

females about to oviposit move out into the leaf litter to find suitable oviposition sites while males are engaged in mating or foraging in the trees at night. Since only 1 or 2 eggs seem ready for oviposition at any time, it is likely that the eggs are evenly distributed in the leaf litter. After mating and oviposition, all but a few adults have died by late June. The larvae, after eclosion, probably develop through July and may go into a diapause. Adults then emerge in late August or September and overwinter.

The life cycle of P. limbata is similar to P. platicollis, but is not in synchrony with P. platicollis. Reproductively mature females are found from late August and probably oviposit in the leaf litter in the same manner as P. platicollis. In P. limbata there is also a difference in the sexual behavior patterns with the males moving about in the trees while ovipositing females are in the litter. Here, also, eggs are probably evenly distributed in the litter. After the last week of July, it appears that the population begins to decrease and by mid-September, the majority of adults have died. However, a few P. limbata adults overwinter and are active in the spring. Whether these adults are reproductively active is unknown.

P. limbata larvae develop from mid-July to late August, and enter an apparent diapause before overwintering. In the spring, development resumes and the larvae pupate in late May or early June with teneral adults being found in late June and July. The overwintering sites for adults or larvae is unknown for both species.

DISCUSSION

Determination of Life Stages

The abundant Pinacodera adults were easily sampled and seasonal activity periods could be established for each species. However, the immature stages were much more difficult to locate. Finding arboreal larvae in the spray samples was misleading since the immature forms of both Pinacodera and Dromius were unknown. In light of this, it was assumed that the smaller larvae were Dromius and the larger, Pinacodera. However, one problem was to relate the comparatively large numbers of adult Pinacodera to low numbers of larvae. Not until first instars were recovered from laboratory held adults was it possible to say that the arboreal larvae were not Pinacodera.

The larval habitat and oviposition sites for the Pinacodera species remained undetermined. King (1919) noted that certain species in the genera Chlaenius, Brachinus and Galerita make mud cells on the leaves and twigs of small trees and shrubs to oviposit in. Examination of spray results and leaves of the oaks did not produce any mud cells or eggs of appropriate size. Generally speaking, the forest was dry and the humidity low. Unprotected eggs laid on bark or leaves of the trees would be subject to dehydration. Although the soil was generally moist enough to prevent dehydration, neither eggs nor larvae were found in the litter around the trees where the ground-dwelling adults were concentrated.

Not until reproductively mature females of both species began appearing in the glycol pitfall traps, did it become apparent that the females moved out into the leaf litter much farther than 1 m from an adjacent tree. Implementation of the additional 60 live traps produced

carabid larvae similar to those larvae reared from adults.

The larvae from the oak spray samples are most likely to be D. piceus. These immatures were compared to drawings of Emden (1942) of a European species of Dromius and the two were very similar. The size of the immatures appears to be appropriate for D. piceus, and since it was discovered that D. piceus pupate in the trees, it is highly likely that the larvae occur there as well.

The Types of Life Cycles

Pinacodera platicollis and P. limbata are examples of "spring breeders" and "summer breeders" as used by Gilbert (1956). It could be argued that since gravid females of P. platicollis were collected in the fall, this species could be classified as an "autumn breeder" as well. However, few females were collected in the fall in pitfall traps, and assuming that fall behavior would be the same as spring, this indicates that oviposition probably does not occur then. P. limbata is mainly a summer breeder even though a few adults appear to overwinter. Luff (1973) warns, however, that in different localities the same species may show different cycles. If this is true, southern populations of both Pinacodera species may have some variation in reproductive timing. However, if both species still occur within the same habitat, asynchronous life cycles should still be expected.

Kurka (1975, 1976) uses a system of breeding types based on diapause as devised by K. Hurka (1973). These types are: 1) main breeding type without larval diapause; 2) main breeding type with larval diapause and variants a) without, and b) with imaginal diapause; and 3) type without diapause. Using this system, evidence points to

the Pinacodera species as spring and summer breeders with diapausing larvae.

Daily and Seasonal Activity

Three patterns of movement developed in the study of the Pinacodera species. Crepuscular climbing of trees leading to a combination of climbing and flying and a peak flight period was noted in the trap catches for P. limbata. The crepuscular activity was found in both species and is likely to be a fixed form of behavior as long as weather conditions are favorable.

This crepuscular movement helps explain why more Pinacodera adults are recovered from white oaks and why more adults are found at the base of the red oaks. As the carabids begin to move down the tree trunks before dawn, they seek out hiding sites for the daylight hours. There are many such locations on white oak trees under the bark scales and few adults have to go to the litter. For red oaks, however, there are many fewer hiding sites and more carabids must move to the leaf litter to find adequate cover.

The second form of movement, nocturnal flying and climbing, while recorded for P. limbata, probably occurs in P. platicollis as well, but to a lesser extent because of the generally cooler temperatures P. platicollis must contend with. As indicated by the results of the dispersal experiment, active nocturnal movement by P. limbata was common and probably constant throughout the summer. This movement in the trees may have functioned in several ways: 1) prevented overcrowding and subsequent food competition; 2) provided a means of locating mates; 3) allowed for the exploitation of new habitats and 4) as nondirected random movement.

Another aspect of the arboreal activity was reflected in the sticky board trap catch. A pattern emerged relating the trap tree and the

presence or absence of an adjacent clearing with the number of beetles collected. Trap trees, either red or white oak, that were at the edge of a small clearing collected more carabids than those trap trees that were surrounded by other trees or adjacent to clear cut areas. There appears to be no influence of trap tree size (DBH), height or species on the trap catch of P. limbata. However, other factors which may influence the trap catch are the number of red and white oaks immediately adjacent to the trap tree and the age class of such trees.

Why the catch for trees adjacent to clearings should draw larger numbers of P. limbata is unknown. Flight behavior data other than the vertical distribution was not collected. Assuming that activity within the canopy is random in areas of continuous foliage, concentrations of beetles may build-up at points where there is a break in the foliage.

Although not recorded for P. platicollis, P. limbata showed a period of increased activity during July of both years. This activity was recorded by pitfall traps, sticky board traps and especially the blacklight trap. Weather records indicate that a combination of high temperatures and relatively heavy rainfall may be responsible for part of this activity. A similar though smaller rise in numbers was recorded for D. piceus in 1977. This trend was not observed with other carabid species collected in the blacklight.

Biotic factors for such dispersal as exhibited by P. limbata are not known. However, Thiele (1977) refers to 2 theories that are much debated. The first, the "overflow hypothesis", is an expression of overcrowding and reflects the density of the population. The second, the "foundation hypothesis", refers to an intrinsic need to disperse as

having selective value for establishment of new populations to preserve the species. In the case of P. limbata, more information is needed before more positive arguments for either hypothesis can be substantiated.

Preferred Sites

In general, the Pinacodera species have been found in mesic areas in Lower Michigan, i.e., dry oak forests. But this habitat is not the same as in other parts of their range. Reeves (personal communication) reports that in New Hampshire, both species are found in maple-beech forests in basic soils. Blatchley (1910) recovered both species from sandy locales in Indiana.

Apparently such abiotic factors of the habitat such as pH of the substrate, temperature, humidity and soil particle size are all important and help determine a particular species' distribution (Thiele 1977). It seems clear that the 2 Pinacodera species studied are forest species. However, more information needs to be collected before any conclusions can be drawn for the present distribution of either species.

Predation

Natural enemies of carabids as listed by Thiele (1977) include birds, insectivorous mammals, amphibians as well as other arthropods such as spiders and ants. All have an effect on natural populations of carabids but to what extent is uncertain. Within this study it is likely that spiders would be important predators of Pinacodera since large crab-spiders were found under bark scales of trees and in the litter as well. Beyond these, considering the mode of existence and the large amounts of defensive fluids carried in the abdomen (1/6 of

its volume), it seems unlikely than mandibulate predators would add significantly to a predatory pressure on adults. For the soft-bodied immatures living in the litter, there are likely numerous predators including other carabids.

The Role of Pinacodera Species

A predatory mode of existence for both species was not proven, but is suggested by natural feeding observations, laboratory feedings and the structure of the proventriculus. The proventricular structure and the length to breadth ratio of the mandibles coincide with the second trophic level of Zhavoronkova (1969) in which most species studied with morphology similar to the Pinacodera species were mainly zoophagous. The Pinacodera species, living in a transitional state between a terricolous and arboricolous existence, are likely to be active predators of litter dwelling insects as immatures and of small, soft-bodied insects in the trees as adults. Adults may supplement their diets with liquid or fermenting plant materials.

Competition

Between the 3 principal lebiine species in the plots, the potential for prey competition would seem high. All 3 species are of approximately the same size and adults have similar habits of climbing trees and flying at night. However, P. platicollis and P. limbata have developed non-synchronous life cycles and so are temporally displaced in their life cycles. For the major portions of these populations, prey competition is lacking with the other species. It appears that even the larvae in the soil do not compete directly for prey since active larvae of one species are moving about while the immatures of the other species are either in a diapause or pupal stage.

Although D. piceus is found in many of the same situations as both Pinacodera species, they seem to prefer drier sites. This preference for slightly different habitats would reduce the competition pressure that might otherwise exist.

Hutchinson (1959) provided numerical constants to determine if additional species can be added to a community without competing with established species (species packing). When these values were compared to the ratios of mandible width, assuming it is the correct character to measure, the values seemed equal to the constants. It would seem that interspecific competition is not present for prey in the adults.

Areas for Continued Research

The life histories for both species, though known overall, need refining. The larval stages of P. platicollis are still unknown and developmental rates and thresholds of both species are lacking. Overall sites of adults and larvae are not precisely known. Adults may aggregate, spending the winter in some protected site. There is no direct evidence for this but the available data indicates that they are not evenly spread in the leaf litter nor are they in the soil and litter adjacent to the trees. Perhaps radioactive tracing of tagged individuals can provide the answers.

The population dynamics and dispersal mechanisms are not known and much more information on both of these subjects need to be studied. Inclusion of sticky board and Malaise traps would provide more complete sampling and data on movement.

APPENDIX

APPENDIX

1. Description of the Pinacodera species

Pinacodera limbata and P. platicollis are similar in appearance and characters often integrate, making positive identification of certain specimens difficult. Both species are rufo-tenaceous to piceous in color though P. platicollis is generally darker. Genitalia are also similar with the aedeagus of the male in P. limbata $1\frac{1}{2}$ times as large as P. platicollis. Generally, P. limbata, approximately 10 mm long, is most easily separated from P. platicollis by having a pale macula on the elytral shoulder and antennae 6 ± 1 mm long. Light or obscure punctuation and rounded hind angles characterize the pronotum of P. limbata (Figure 1).

P. platicollis, averaging 11 mm, may or may not have an indistinct macula on the elytral shoulder region and antennae are shorter, 5 ± 1 mm. The pronotum is more coarsely punctate and the hind angles are more prominent than P. limbata.

2. Stand characteristics of the plots

a) Density of trees and stand composition

Table 2.1. The basal area and density of trees in the Branch Mature and Branch Pole plot areas within the Manistee National Forest near Baldwin, Michigan, 1977.

<u>Quantity Measured</u>	<u>Sites Sampled</u>	
	<u>BP</u>	<u>BM</u>
basal area per hectare (cm^2/ha)	206,220	186,780
trees per hectare	1,329	736
mean DBH (cm)	13.4	18.9

Table 2.2 The percentage of basal area of the dominant oak species within the plot areas of Branch Mature and Branch Pole within the Manistee National Forest near Baldwin, Michigan, 1977.

<u>% of basal area</u>	<u>BP</u>	<u>BM</u>
red oak	55.0	12.5
white oak	40.0	32.5
other	5.0	55.0

b) Floral inventory of the plots

Table 2.3 Plant species found within the Branch Mature and Branch Pole plots in the Manistee National Forest near Baldwin, Michigan, 1977. These plants are common to both plots though in varying numbers.

	<u>Common Name</u>	<u>Scientific Name</u>
<u>Woody</u>	white oak	Quercus alba Linnaeus
	red oak	Quercus rubra Linnaeus
	red maple	Acer rubrum Linnaeus
	bigtooth aspen	Populus grandidentata Michaux
	black cherry	Prunus serotina Michaux
	sassafras	Sassafras albidum (Nutt) Nees
	blueberry	Vaccinium sp.
	witch hazel	Hamamelis virginiana Linnaeus
	dogwood	Cornus florida Linnaeus

Table 2.3 (cont'd.)

<u>Herbaceous</u>	bracken fern	<i>Pteridium aquilinum</i> (L.) Kuhn
	wintergreen	<i>Chimaphila</i> sp.
	crab grass	<i>Digitaria</i> sp.
	peppergrass	<i>Lepidium</i> sp.
	fescue	<i>Festuca</i> sp.
	dropseed	<i>Sporobolus</i> sp.
	panicum	<i>Panicum</i> sp.
	rice grass	<i>Oryzopsis racemosa</i> (Ricker) Smith
	trailing arbutus	<i>Epigaea ripens</i> Linnaeus

3. Soil characteristics of the plots

Table 3.1 Soil characteristics of Branch Mature and Branch Pole plots in the oak-dominated Manistee National Forest, northwest of Baldwin, Michigan, 1977.

<u>Site</u>	<u>pH</u>	<u>Composition</u>			<u>% organic matter</u>
		<u>% sand</u>	<u>/ % silt</u>	<u>/ % clay</u>	
Branch Mature	4.4	81.5	8.1	10.4	3.9
Branch Pole	4.6	80.5	8.5	11.0	4.4

LITERATURE CITED

LITERATURE CITED

- Anderson, John. Professor of Entomology, University of California, Berkeley, California.
- Ball, George E. Professor of Entomology, University of Alberta, Edmonton, Alberta, Canada.
- Blatchley, W. S. 1910. The Coleoptera of Indiana. Bull. Ind. Dept. Geol. and Nat. Res. 1. Indianapolis, p. 1-1385.
- Casey, T. L. 1920. Memoirs of the Coleoptera. The New Era Printing Co., Lancaster, Pennsylvania, 9: 1-529.
- Dunbar, W. F. 1955. Michigan Through the Centuries, Vol. 1. Lewis Historical Publishing Co., Inc., New York, New York, p. 1-502.
- Emden, F. I. van. 1942. A key to the genera of larval Carabidae. Trans. Roy. Ent. Soc. London, 92: 1-99.
- Erwin, Terry, Donald R. Whitehead and George E. Ball. 1977. North American Beetle Fauna Project, Family 4. Carabidae, the Ground Beetles. World Digest Publications, Oxycopsis Pond, Wallace Road, Kinderhook, New York, p. 1-68.
- Forsyth, D. J. 1972. The structure of pygidial defense glands of Carabidae. Trans. Zool. Soc. Lond. 32: 249-309.
- Gilbert, Owen. 1956. The natural histories of four species of Calathus living on sand dunes in Anglesey, North Wales. Oikos 7(1): 22-47.
- Horn, George. 1881. On the genera of Carabidae with special reference to the fauna of boreal America. Trans. Am. Ent. Soc. 8. Philadelphia, P.XIX. p. 91-196.
- _____. 1882a. Synopsis of the species of the Tribe Lebiini. Trans. Am. Ent. Soc. 10. Philadelphia, p. 126-164.
- Hubbard, H. G. and A. E. Swartz. 1878. Coleoptera of Michigan. Proc. Amer. Phil. Soc. 17. Philadelphia, p. 627-666.
- Hurka, K. 1971. Entwicklungstypen der mitteleuropaischen Carabus-Arten in ihrer Beziehung zu den endogenen und exogen Faktoren. Proc. 13th Int. Congr. Ent. Moskva 1968, I, p. 501-502.

- Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *The Amer. Nat.*, 93(870): 145-159.
- King, J. L. 1919. Notes on the biology of the carabid genera Brachynus Galerita and Chlaenius. *Ann. Ent. Soc. Am.* 12(4): 382-388.
- Kurka, Antonin. 1975. The life cycle of Bembidion tibiale. *Acta Ent. Bohemoslav* 72(6): 374-382.
- _____. 1976. The life cycle of Agonum ruficorne (Goeze). *Acta Ent. Bohemoslav*, 73: 318-323.
- Liebherr, James and Joseph Mahar. 1978. The carabid fauna of the upland oak forests in Michigan: Survey and analysis. In preparation.
- Lindroth, Carl H. 1954. Carabid Beetles of Nova Scotia. *Can. Ent.* 86. Ottawa, p. 299-310.
- _____. 1966. The ground beetles of Canada and Alaska. *Opusc. Ent.*, suppl., 34: 945-1192.
- Luff, M. L. 1973. The annual activity pattern and life cycle of Pterostichus madidus (F).
- Reeves, Marcel. Professor of Entomology, University of New Hampshire, Durham, New Hampshire.
- Surgeoner, Gordon A. 1975. The life history and population dynamics of the variable oakleaf caterpillar, Heterocampa manteo (Dblly) in Michigan. PhD. Thesis, Michigan State University.
- Taylor, L. R. 1960. Distribution of insects at low levels in the air. *Jour. Anim. Ecol.* 29: 45-63.
- Thiele, Hans-Ulrich. 1977. Carabid Beetles in Their Environments. Springer-Verlag, Berlin, Heidelberg, New York. p. 369.
- Townes, Henry. 1972. A lightweight Malaise trap. *Ent. News* 83: 239-247.
- Zar, Jerrold H. 1974. Biostatistical Analysis. Prentice Hall, Inc., Englewood Cliffs, New Jersey, p. 620.
- Zharonokova, T. N. 1969. Certain characteristics in the structure of beetles in the relation to the character of their feeding. *Ent. Obozorne* 48(4): 729-744. (In Russian)

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