This is to certify that the

thesis entitled

Activity patterns in some species of deciduous forest litter Carabidae (Coleoptera) in Michigan's Upper Peninsula

presented by

Judy Mousigian Nesmith

has been accepted towards fulfillment of the requirements for

M.S. degree in Zoology

Richard J. Snider

Major professor
Richard J. Snider

Date Feb. 21, 1985

ACTIVITY PATTERNS IN SOME SPECIES OF DECIDUOUS FOREST LITTER CARABIDAE (COLEOPTERA) IN MICHIGAN'S UPPER PENINSULA

by
Judy Mousigian Nesmith

A Thesis
Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE
Department of Zoology
1985

3346675

ABSTRACT

ACTIVITY PATTERNS IN SOME SPECIES OF DECIDUOUS FOREST LITTER CARABIDAE (COLEOPTERA) IN MICHIGAN'S UPPER PENINSULA

by

Judy Mousigian Nesmith

Pitfall traps were used to survey Carabidae (Coleoptera) in a deciduous woodlot in Michigan's Upper Peninsula. Five species of carabids were selected for analysis. Seasonal and diel activity patterns of Calathus ingratus Dejean, Pterostichus coracinus Newman, P. melanarius Illiger, P. pensylvanicus Leconte, and Sunuchus impunctatus Say were assessed. Effects of temperature, trapping date and gender upon activity patterns were investigated for each species.

The species studied displayed predominantly nocturnal behavior, though each had some incidence of diurnal activity. Temperature/activity relationships varied between species. Increases in overall activity corresponded closely with these species breeding seasons. In most species, diurnal activity and female activity peaked during periods of reproduction. The necessity for individuals, especially females, of each species to seek extra food, mates, and breeding and oviposition sites is thought to have contributed to increased carabid activity during breeding seasons in this study, and to have induced diurnalism in these normally nocturnal species.

To my parents, in appreciation for

their love and wisdom.

ACKNOWLEDGEMENTS

I wish to thank Dr. R. J. Snider for serving as chairman of my guidance committee. Thanks are also due to Drs. R. Fischer and M. M. Hensley who served as members of my guidance committee.

I also wish to thank Gary Dunn of the MSU Cooperative Extension Service for verifying and correcting my identifications of carabid specimens.

Special appreciation is extended to the Zoology Department office staff for their wonderful help and good humor through the years.

Most of all, I wish to extend my deepest appreciation to my family and friends, and especially my husband Neron, for their love, support, and understanding.

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (Continued)

TABLE OF CONTENTS

INTRODUCTION AND LITERATURE REVIEW

Rhythmic periodicity is prevalent throughout the animal kingdom (Calhoun, 1944). Proper timing of activity in insects is of particular importance. Appearance of adults and larvae must frequently coincide with availability of suitable food supplies and reproduction must be synchronized correctly to ensure that resistant life stages are present during unfavorable seasonal conditions.

Carabid beetles, like many insects, show both daily and seasonal patterns of activity. Among the first to document periodicity in carabid beetles were Park and Keller (1932) and Krumbiegel (1932). Since then, under both laboratory and field conditions, rhythmic activity patterns have been reported in carabids by numerous investigators (Calhoun, 1944; Williams, 1959; Greenslade, 1963; Grum, 1966; Breymeyer, 1966a,b; Thiele and Weber, 1968; Kirk, 1971b; Dondale et al., 1972; Luff, 1978; Baars, 1979, Boiteau, 1983; Boucher and Malausa, 1984).

Various techniques have been used to assess carabid activity patterns. Laboratory research has been conducted using both direct observations and actographs under natural and artificial light-dark regimes (Williams, 1959; Grum, 1966; Thiele, 1977a,b; Boucher and Malausa, 1984). Actographs and observations of beetles in enclosures have also been used in field studies (Greenslade, 1963; Dennison and Hodkinson, 1984b). Kirk (1971b) observed beetles in their natural habitat. Finally, Baars (1979) captured, marked, and radioactively tagged beetles, then followed their movements after release at their capture site.

The majority of carabid activity studies were assessed by pitfall trapping. A few investigators have used time-sorting pitfall traps (Williams, 1959; Dondale et al., 1972; Luff, 1978; Stubbe et al., 1984). These traps have a clock-driven mechanism to partition catches by time increments. Most researchers, however, use a buried trap design (Greenslade, 1965; Barlow, 1970; Jones, 1979; Levesque et al., 1979; Desender and Maelfait, 1982; Dennison and Hodkinson, 1984a,b).

Definite diel patterns of activity were reported for many of the species studied. Greenslade (1963) classified diel activity into three well-defined patterns - nocturnal, diurnal, and plastic. Later, Thiele and Weber (1968) summarized diel activity among carabid beetles in a comprehensive literature review. They concurred with Greenslade's proposed classification, and reported that, of the species investigated, 60% were strictly nocturnal, 22% were mainly day-active, and 18% showed intermediate behavior. Plastic, or intermediate carabid beetles exhibited varying degrees of diurnalism or nocturnalism in response to different environmental conditions.

Frequently, seasonal reproductive rhythms are associated with diel activity patterns (Thiele and Weber, 1968). Thiele (1977c) reports that Larsson (1939) and Lindroth (1949) were among the first researchers to recognize different types of carabid seasonality. Greenslade (1965) simplified their definitions and divided carabid seasonality into three types: 1) spring breeders, 2) summer and summer-autumn breeders, and 3) autumn breeders. Subsequent research has revealed annual reproductive and activity patterns for many species (Johnson et al., 1966; Barlow, 1970; Kirk, 1971a,b; Levesque et al., 1979; Desender et al., 1981; Desender, 1983; and Dennison and Hodkinson, 1984a). Paarman (1979) later expanded Greenslade's categories to include the annual rhythms of species from tropic and sub-tropic areas.

Despite previous studies, mechanisms regulating rhythmic activity patterns are not clearly understood. Activity patterns are most often manifestations of an endogenous periodicity (Saunders, 1982). Frequently, other factors override autonomous control and readjust patterns of activity (Beck, 1980; Saunders, 1982). Rythmicity in carabid beetles is particularly malleable by other factors, and varies widely between species (Thiele and Weber, 1968; Thiele, 1977c).

Carabid beetles in Michigan's mostly forested Upper Peninsula are poorly known, especially in its western half. The only surveys conducted in this area were by Hubbard and Schwarz (1878) and Andrews (1921). Neither were extensive and few carabids were reported. It is the purpose of the following study to supplement the distributional records of Carabidae in Michigan, and contribute to the limited available knowledge of the habits of North American forest carabids.

In summary, the following study:

1. surveyed using pitfall traps, and identified the surface-active Carabidae in a deciduous woodlot in

Dickinson County, Michigan.

2. documented the diel activity patterns of the most common carabid species encountered.

3. investigated the relationship between activity patterns, temperature, and trapping date.

4. examined differences in activity patterns between species and between sexes of the same species.

This study was part of an ecological monitoring program for the United States Department of Defense' Extremely Low Frequency (ELF) Communications System. Portions of this program were subcontracted to Michigan State University from IIT Research Institute, which, in turn, was contracted by United States Naval Defense. This study was included in task 5.3 - Soil and Litter Arthropoda.

MATERIALS AND METHODS

EXPERIMENTAL AREA

This study was conducted on state land in the western end of Michigan's Upper Peninsula, T43N, R29W, S8 (Figures 1,2). The site encompassed about two acres and was approximately seven miles east of the town of Channing in Dickinson County.

This area is part of the Canadian shield, a region of the Upper Peninsula where strong precambrian bedrock is close to the surface and the topography is typically characterized by high hills and deep valleys. Glaciation has left a layer of glacial till on top of this bedrock (Dorr & Eschman, 1970).

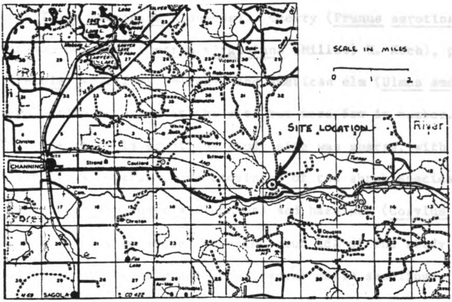
The soil at the study site was thin, undeveloped below 20 inches, and rocky, moderately well to well-drained, with a humus layer of only 2-3 inches. It typed out as an Emmet fine sandy loam[1].

The area was once covered by dense white and red pine forest. However, subsequent logging, which reached its peak in the 1890s, has eliminated this forest association (Santer, 1977). The study site was last logged between 1964 and 1969 and is now a mature hardwood forest[2].

Tree density at the site was approximately 11 trees per $100m^2$. Sugar maple (*Acer saccharum* Marshall) was by far the most prevalent tree species, but the largest trees at the site were

1,2. The author is indebted to Walt Summers of the U.S. Soil Conservation Service in Iron Mountain, MI, for providing information about the soil and history of the study area.

Figure 1. Dickinson County, Michigan. ⊙ marks research site.



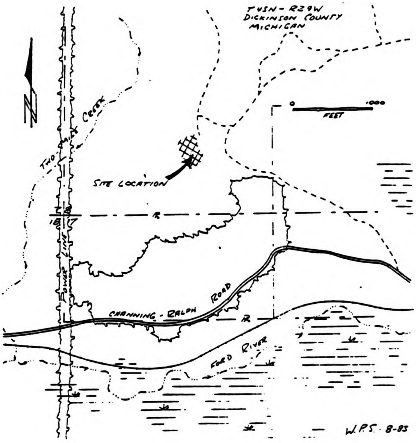


Figure 2. Location of study area.

basswood (Tilia americana Linnaeus). Cherry (Prunus serotina Ehrhart), American hop-hornbeam (Ostrya virginiana (Miller) K. Koch), paper birch (Betula papyrifera (March)) and American elm (Ulmus americana (Linnaeus)) also occurred at the site but were few in number.

The understory layer at the study site was sparse, with approximately 6% coverage, and consisted of two shrub species, leatherwood (Dirca palustris Linnaeus) and hazelnut (Corylus sp.).

Herb cover was moderate, covering abut 28% of the study area, and, out of 20 different plant types, sugar maple seedlings, sedges (Cyperaceae), wild lily of the valley (Maianthemum canadense Desfontaines), and sweet cicely (Osmorhiza claytoni (Clarke) were most prevalent. Yellow violet (Viola pubescens Aiton), American hop-hornbeam seedlings, and spikeweed (Aralia racemosa Linnaeus) were also common. The formulae used to calculate plant density or coverage are given in Appendix A.

SAMPLING

Samples were taken using 40 randomly placed pitfall traps, 20 in each of two adjacent areas at the study site. Sampling periods encompassed twenty-four hours. Half of the traps were used to collect separate night and day samples. These traps were set at dusk and changed and refilled the following dawn. The second sample was collected at dusk the same day. The remaining traps were set at dusk and collected at dusk the next day. Traps were covered between sampling periods. Samples were collected in this manner weekly from May through October, 1983, for a total of twenty-five sampling dates. No sample was taken the third week of October due to severe weather. The sampling schedule is provided in appendix B.

Adis (1979) summarized the problems associated with pitfall trapping for arthropods and suggested that pitfall trap results should be interpreted with caution. Problems arise in separating the density and activity components of a given population. However, Briggs (1961) and Greenslade (1964) found that pitfall trapping was useful in studies of carabid beetles for assessing strictly locomotor activity. Thiele (1977c) reports that for analysis of daily and annual activity rhythms, pitfall trapping is superior to any other method. Further studies have shown that pitfall trapping may be the best method for investigating carabid community composition. Kirk (1971b) compared pitfall trapping to soil sampling and direct observation in cropland species. Pitfall trapping produced the same number of species in similar ratios of abundance as the other sampling methods. Uetz and Unzicker (1976) investigated pitfall trapping and quadrat litter sampling efficiencies in assessing populations of woodland cursorial spiders. Dennison and Hodkinson (1984b) conducted similar research on carabid and staphylinid beetles. Both studies showed that pitfall trapping provided a more complete faunal list of cursorial arthropods than quadrat sampling.

The pitfall traps used in this study were made of smooth white plastic and consisted of three parts; a large cup which functioned as an outer sheath, a smaller cup which fitted snugly inside the large cup, and a funnel that rested on the rim of the large cup (figure 3). The funnel was used to help retain trapped beetles in the small inner cup, and to reduce incidence of disruption by other animals. Holes were punched into the bottom of the large cup and

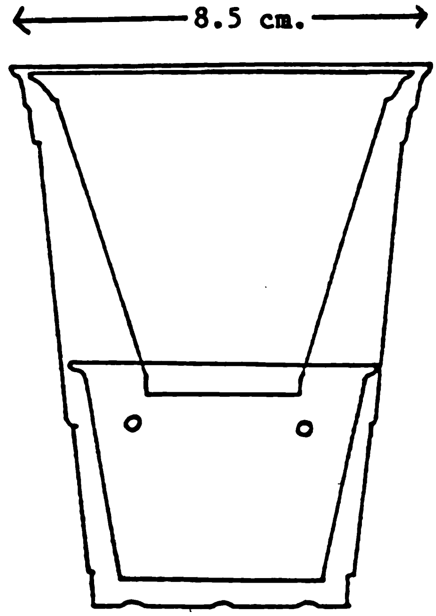


Figure 3. Diagram of Pitfall Trap

sides of the small cup for drainage. Clear plastic cups upended over the pitfall traps served as covers when the traps were not in use.

Traps were buried with rims flush with the soil surface. They were then covered and left undisturbed for a week. This served to eliminate "digging-in effect", a phenomenon in which disturbance and raised CO_2 levels in the soil caused by placing traps create artificially high levels of arthropod activity for the following two days (Joosse and Kapteijn, 1968). Traps were set by filling the inner cup with approximately 2.5 centimeters of ethylene glycol, which acted as a trapping agent and temporary preservative. Changing traps was simply a matter of replacing the inner cup with a fresh cup and refilling with ethylene glycol.

SORTING

A solution of 95% ethyl alcohol with 1% glycerin was used to rinse samples through a fine mesh sieve (U.S. Standard sieve series #2000) and for subsequent storage. Samples were later sorted and carabids were pinned and identified to species using Lindroth's (1969) system of classification. Sex and stage of adult (teneral or mature) were also identified and recorded along with number of individuals. Teneral adults were recognized by their pale, soft exoskeleton. Adult carabids generally remain teneral for approximately 2-3 days after pupal eclosion (Goulet, 1974). Voucher specimens are deposited in the Entomology Museum of Michigan State University.

WEATHER DATA

Temperature data were obtained from the National Weather service. Minimum and maximum daily temperatures were recorded at the Way Dam weather station situated approximately twelve miles west of the study area (figure 4). Minimum daily temperatures for night catch regressions were obtained by averaging minimum temperatures of the two adjacent dates of the trapping period. For example, minimum daily temperatures of May 4th and 5th were averaged to obtain the minimum temperature used for the night catch of that sampling date. Minimum and maximum temperatures used for regression analyses are listed in appendix C.

Humidity data were not available from the Way Dam weather station. A few weeks of humidity data, however, were obtained from a hygrothermograph situated at the site which functioned intermittently. These data are tabled in appendix D.

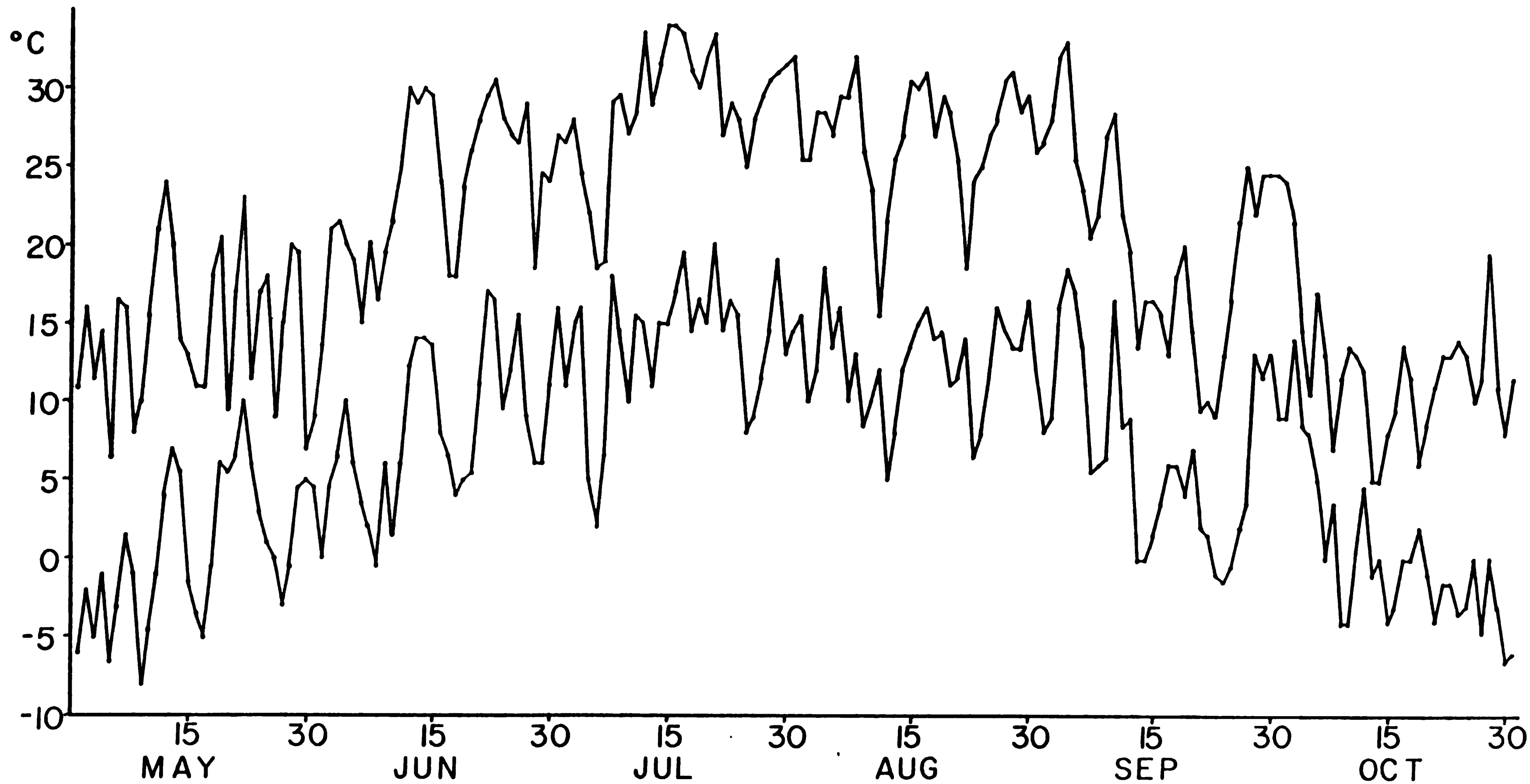


Figure 4. Minimum and maximum daily temperatures recorded at the Way Dam weather station from May, 1983 through October, 1983.

STATISTICAL ANALYSIS

Analyses of variance (using an ANOVA computer program SPSS version 8.3, 1984), linear regression analyses, and T- and q- tests of comparisons were used to compare catch size with gender, date, diel effects, and temperature. Only species caught in sufficient numbers for these analyses (5% of more of the total catch) were examined. For statistics comparing diel effects, numbers caught per sample were converted to numbers caught per hour to account for the changing lengths of day and night through the season. A list of length of night and day trapping periods is presented in appendix E. Data for the ANOVA statistics were log-transformed so that they would be approximately normally distributed. The remaining statistics were hand-calculated using procedures and formulae from Sokal and Rohlf (1981). Accepted significance for statistical results was $p = 0.05$ or less.

Numbers per sample and numbers caught per hour were separated into male/female and night/day components for each species (appendices F and G). Seasonal means were calculated and compared using T- and q-tests. Number of individuals and numbers caught per hour were plotted against trapping date to display shifts in diel and seasonal activity. Occurrence of teneral adults was indicated to identify periods of recruitment.

Catches per trapping date were regressed on temperature for that date for each species. Night catches were regressed on minimum night temperatures and day catches regressed on maximum day temperatures based on Baar's (1979) conclusions that minimum temperatures were significant to night-active species, while day active species were influenced more by maximum temperatures. Catches for each species were analysed in two-month sections (n=9 in the spring months, n=8 in each of the remaining sections). This procedure served to reduce the confounding effects of seasonal influences on activity.

RESULTS AND DISCUSSION

GENERAL RESULTS

Eighteen different species of Carabidae were collected from May 1983 through October 1983. Examination of museum records showed that ten species had not previously been recorded as occurring in Dickinson County. A list of these species is provided in Table 1. Inspection of catch data showed five species caught in far greater numbers than the others. *Calathus ingratus* Dejean, *Pterostichus coracinus* Newman, *P. melanarius* Illiger, *P. pensylvanicus* Leconte, and *Synuchus impunctatus* Say each contributed over 5% to the total catch. Individuals of *P. pensylvanicus* alone made up over a third of the total catch. Together, these species comprised over 90% of all carabids trapped. These species were selected for further analysis.

All selected species belong to the tribe Pterostichini and are commonly found in North American forest habitats. *P. melanarius* is an introduced European species and is also common in fields and arable land (Lindroth, 1969; Barlow, 1970; Ericson, 1977; Jones, 1979). The remaining species are native to North America (Lindroth, 1969).

Activity in each of these selected species as determined by number trapped, was assessed and compared with a variety of factors. Data on these carabid beetles activity patterns, some possible influences on activity, and variation of activity between species will be discussed in the following pages.

SEASONAL ACTIVITY

Each carabid species examined displayed a distinct seasonal

Table 1. List of carabid species collected by pitfall trapping in the study area with number of individuals of each species. An * denotes species that are new records for Dickinson County.

species	number of individuals caught
Agonum decentis Say	1
**A. placidum* Say	1
A. retractum Leconte	19
**Bembidion quadrimaculatum oppositum* Say	1
Calathus gregarius Say	57
**C. ingratus* Dejean	206
Clivina fossor Linne	3
**Cymindis cribricollis* Dejean	9
Harpalus fuliginosus Duftschmid	24
Myas cyanescens Dejean	12
**Notiophilus aeneus* Herbst	3
**Pterostichus adstrictus* Eschscholtz	6
P. adoxus Say	3
**P. coracinus* Newman	131
P. melanarius Illiger	108
P. pensylvanicus Leconte	526
**Sphaeroderus lecontei* Dejean	1
**Synuchus impunctatus* Say	272
TOTAL	1383
# of species	18

pattern of activity during 1983 (Figures 5-9). Occurrence of teneral adults indicated periods of recruitment (e.g. additions of new adults to the adult population) for each species.

Seasonal data for P. melanarius and P. coracinus showed activity beginning in May, gradually increasing during the summer months, and declining in September. Activity of P. melanarius lagged a few weeks behind that of P. coracinus (Figures 5,6). Teneral adults of both species were caught in July, several weeks after activity began.

S. impunctatus also was most active during summer. Activity in this species, however, started in late June, rose sharply to a peak in July, and ended by early September (Figure 7). Tenerals made up the entire first catch in June.

Activity of another summer-active species, C. ingratus, began in mid-June, peaked during August, and continued through late October (Figure 8). Tenerals first appeared in late July, but most were caught in August.

Seasonal activity of P. pensylvanicus differed greatly from the other species studied (Figure 9). The majority of P. pensylvanicus were caught in May, June and July, and declined abruptly in August. A secondary activity peak occurred in autumn. Teneral adults were present only during this second peak.

The seasonal activity patterns shown by the species in this study corresponded closely with patterns and information documented in previous investigations (Briggs, 1961); Greenslade, 1965; Barlow 1970; Levesque et al, 1979; Jones, 1979). Although onset of activity may have varied by a few weeks depending upon temperature

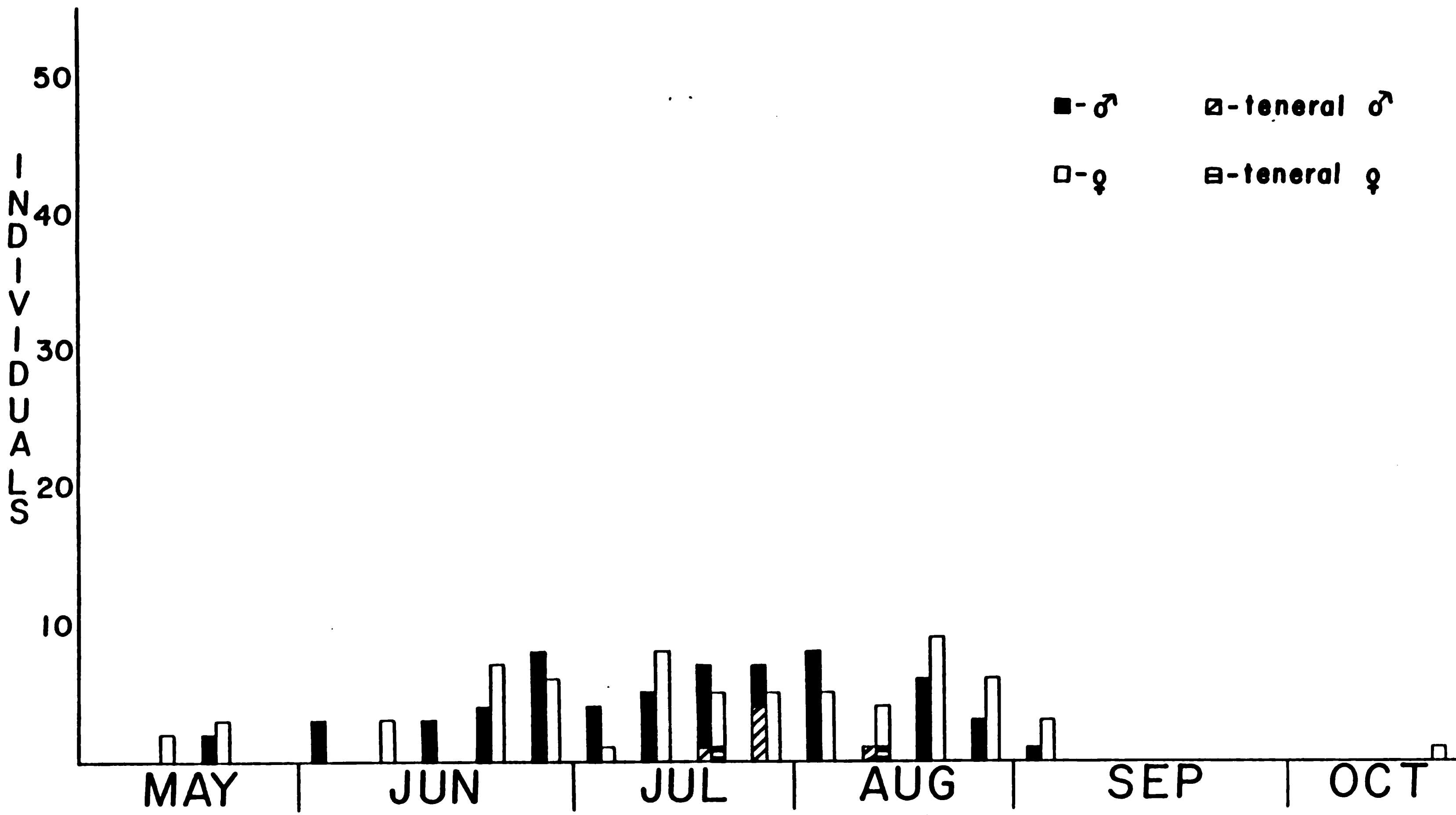


Figure 5. Number of male, female and teneral individuals of P. melanarius caught per trapping date.

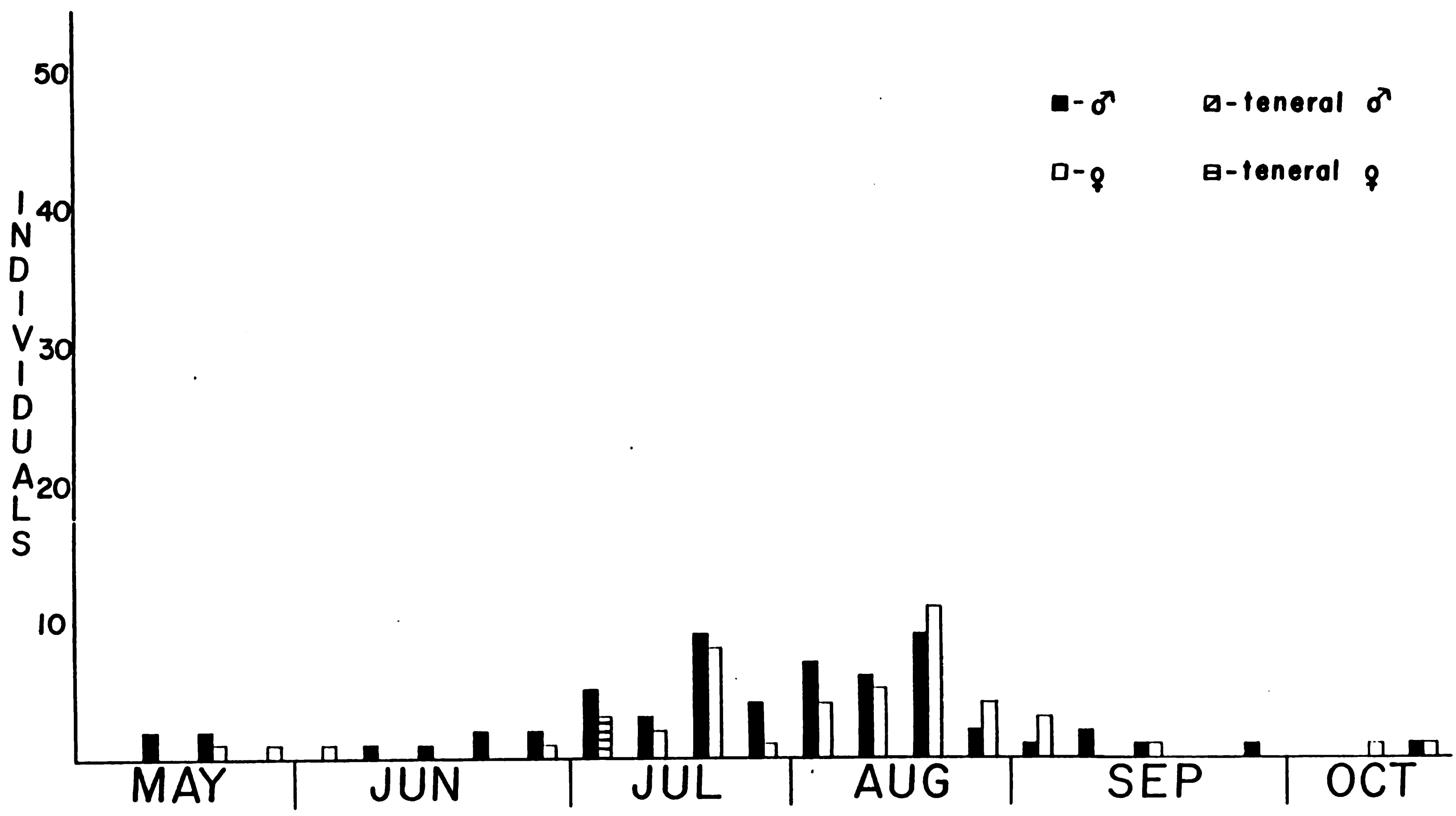


Figure 6. Number of male, female and teneral individuals of P. coracinus caught per trapping date.

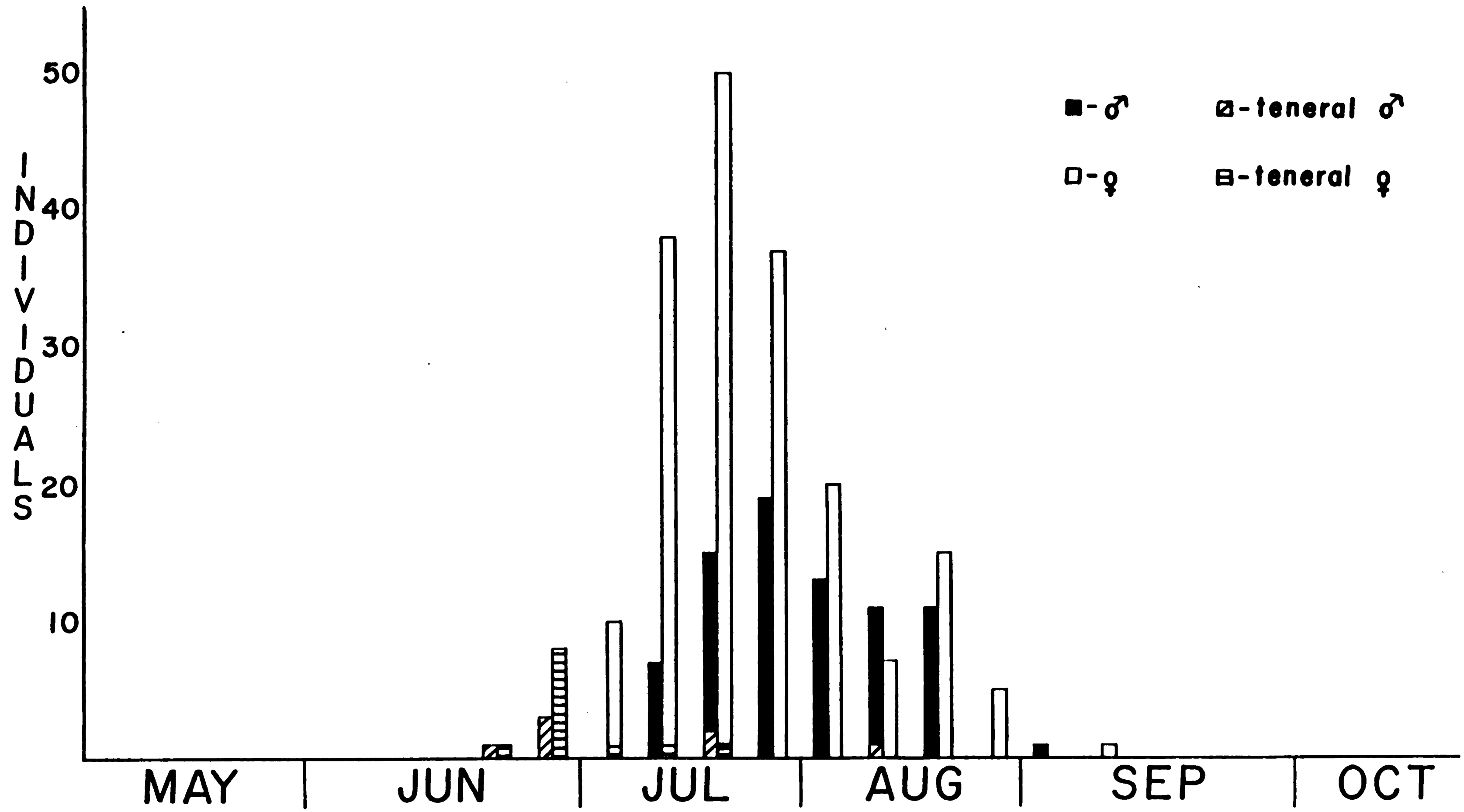


Figure 7. Number of male, female and teneral individuals of <u>S. impunctatus</u> caught per trapping date.

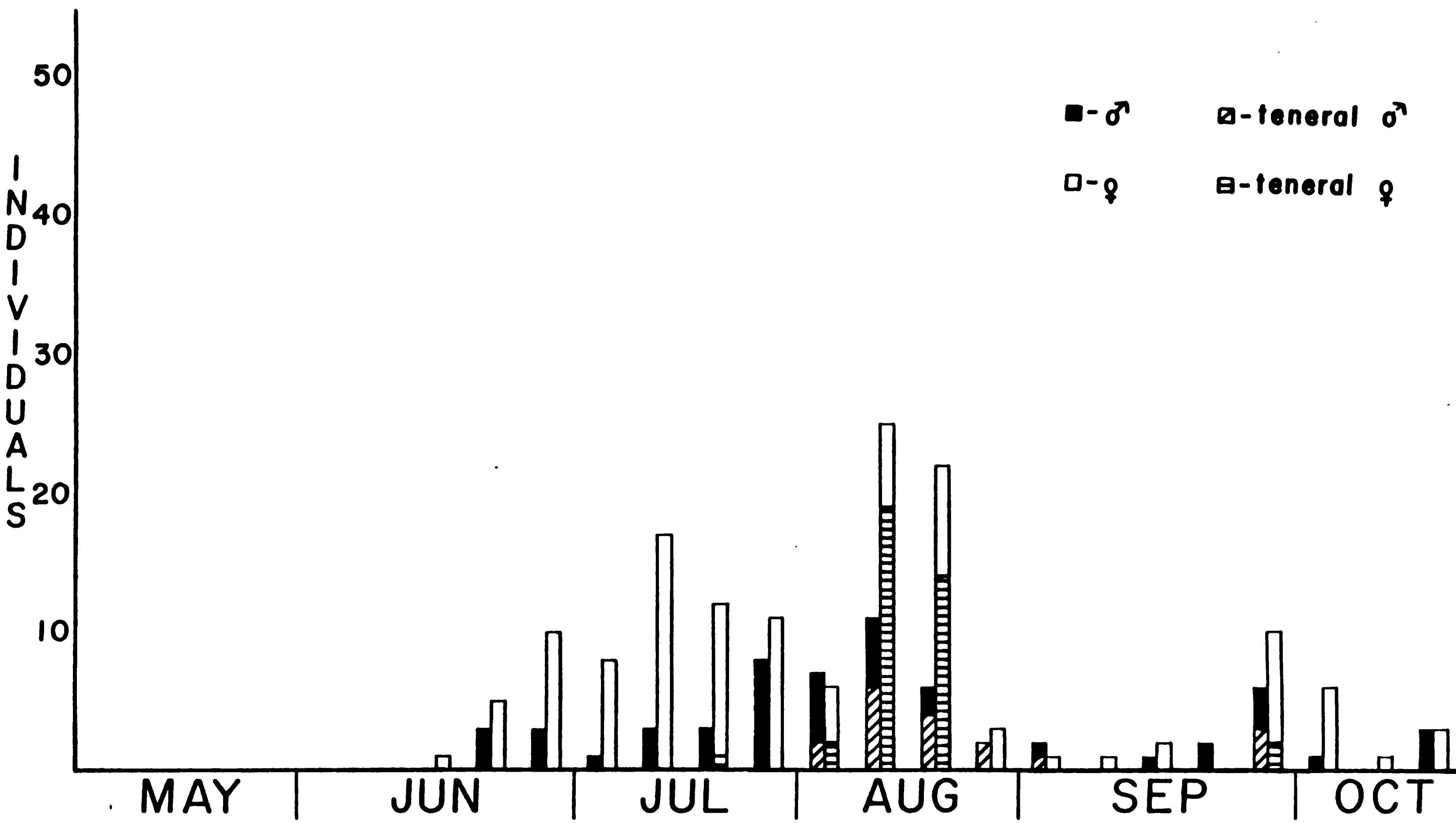


Figure 8. Number of male, female and teneral individuals of C. ingratus caught per trapping date.

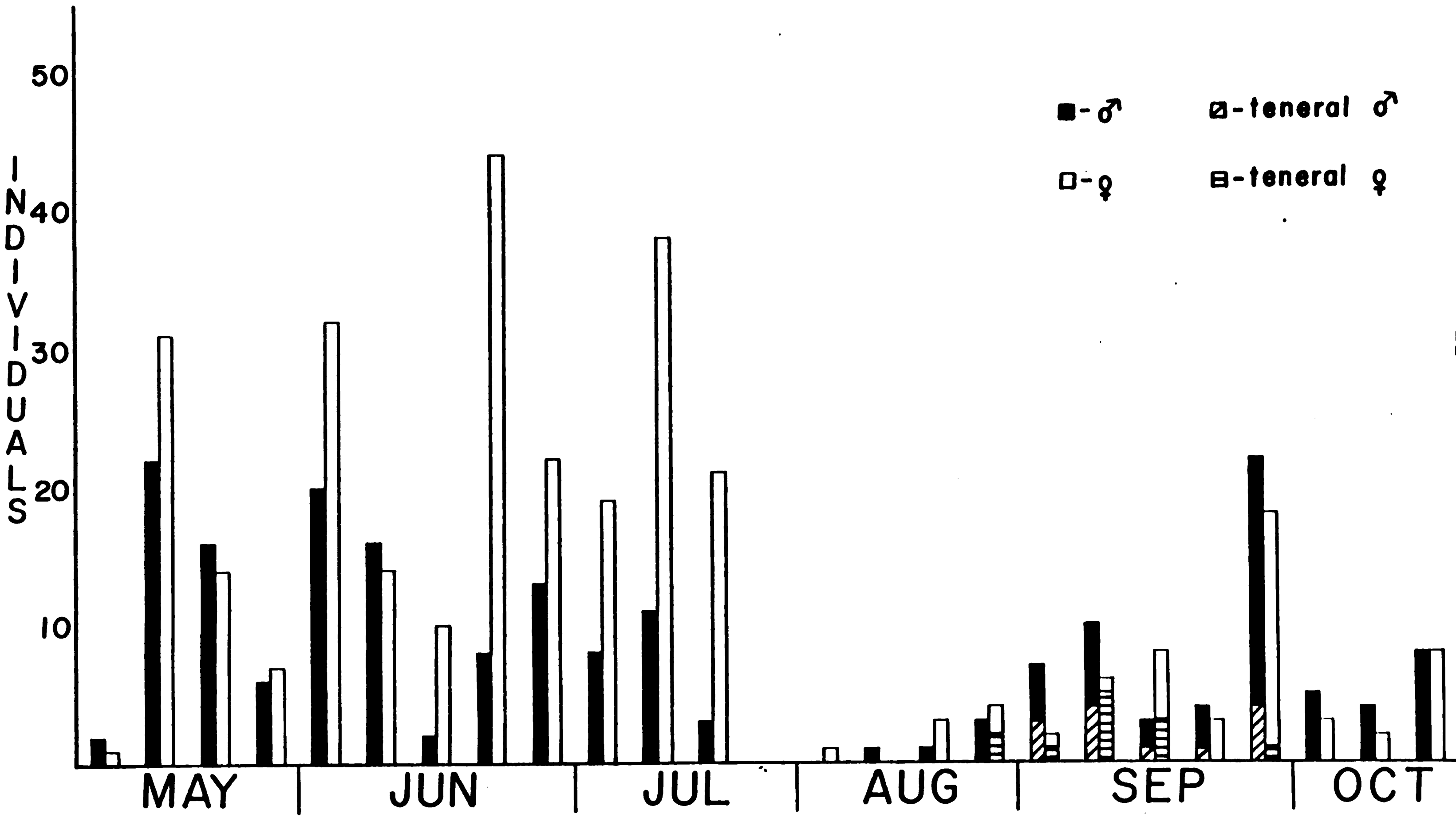


Figure 9. Number of males, females and teneral individuals of P. pensylvanicus caught per trapping date.

habitat or geographic location (Barlow, 1970; Thiele, 1977c), the seasons during which activity peaks and declines occurred usually remained consistent.

Seasonal activity peaks in carabids generally coincide with their breeding season (Barlow, 1970; Thiele, 1977c; Levesque et al, 1979). Indeed, summer-active species in this study, P. melanarius, P. coracinus, and S. impunctatus have been identified in previous studies as summer-breeders that primarily overwintered as larvae, emerging as adults the following season to breed (Greenslade, 1965; Lindroth, 1969; Barlow, 1970; Levesque et al, 1979; Jones, 1979). Some authors have reported that spent adults (those that have already reproduced) of P. melanarius and P. coracinus also overwinter and breed a second year (Greenslade, 1965; Lindroth, 1969; and Barlow, 1970). In this study, P. melanarius and P. coracinus adults caught early in the season, before tenerals emerged, may have included second year breeders. Second year adults have not been reported to occur in populations of S. impunctatus. Lindroth (1969) writes that this species overwinters exclusively as larvae, a statement corroborated by early occurrence of tenerals in this study.

Little is recorded on C. ingratus reproductive patterns. It is reasonable to assume, however, that this summer-active species is also a summer breeder. The delayed emergence of tenerals in this study, coupled with Lindroth's (1969) claim that both C. ingratus larvae and adults overwinter, suggests that second year breeding adults occurred in this species as well.

P. pensylvanicus seasonality differs from that of the other four species examined in this study. Barlow (1970), Goulet (1974), and Levesque et al (1979) agreed that P. pensylvanicus is a spring-breeding species that overwinters as an adult. Barlow attributed summer declines of activity to mortality of post-reproductive adults, but did not rule out the possibility that some adults from spring may aestivate. Goulet (1974) documented that some spent P. pensylvanicus adults underwent summer aestivation and resumed activity during fall before hibernating a second winter. Barlow (1970) concluded that the fall activity peak did not represent reproductive activity, but was due to newly emerged adults seeking food and hibernation sites. Goulet (1974) generally concurred with Barlow, but also suggested that some young adults may mate during fall and females would not oviposit until spring. The presence of teneral P. pensylvanicus adults only in late August and September indicated that recruitment occurred during fall in this study. Furthermore, non-teneral adults which occurred a few weeks before teneral emergence may have been second year adults.

TEMPERATURE EFFECTS

Comparisons of night and day carabid activity to minimum night and maximum day temperatures yielded varying results between species (Table 2). Night activity significantly increased as night minimum temperatures increased for P. coracinus and S. impunctatus (Figures 10, 11). No well-defined relationships however, were found between temperature and activity levels for P. melanarius and C. ingratus (Figures 12, 13), although activity in C. ingratus appeared to be inhibited at cool temperatures. P. pensylvanicus activity, compared with temperatures during both its spring and

Table 2. Regression statistics of weekly night and day trap catches of the 5 most common species of Carabidae collected within the study area regressed on minimum and maximum temperatures in °C. Catches were separated by season and regressed separately for each species to avoid seasonality effects. An * denotes accepted significance at P≤.05.

Species	Source of variation	Sum of squares	Degrees of freedom	Mean square	F statistic
P. pensylvanicus spring night	explained-due to linear regression	.39	1	.39	.008
	unexplained-error around regression line	363.83	7	363.83	
spring day	explained	79.98	1	79.98	9.08*
	unexplained	61.58	7	8.80	
fall night	explained	291.57	1	291.57	7.10*
	unexplained	246.40	6	41.07	
fall day	explained	3.45	1	3.45	.70
	unexplained	29.40	6	4.90	
P. coracinus summer night	explained	37.31	1	37.31	7.94*
	unexplained	28.20	6	4.70	
summer day	explained	.49	1	.49	.46
	unexplained	6.39	6	1.07	
P. melanarius summer night	explained	12.46	1	12.46	.97
	unexplained	77.54	6	12.90	
summer day	explained	15.20	1	15.20	2.36
	unexplained	38.68	6	6.45	
S. impunctatus summer night	explained	222.30	1	222.30	9.16*
	unexplained	145.70	6	24.28	
summer day	explained	4.23	1	4.23	.81
	unexplained	31.27	6	5.21	
C. ingratus summer night	explained	52.34	1	52.34	.81
	unexplained	387.54	6	64.59	

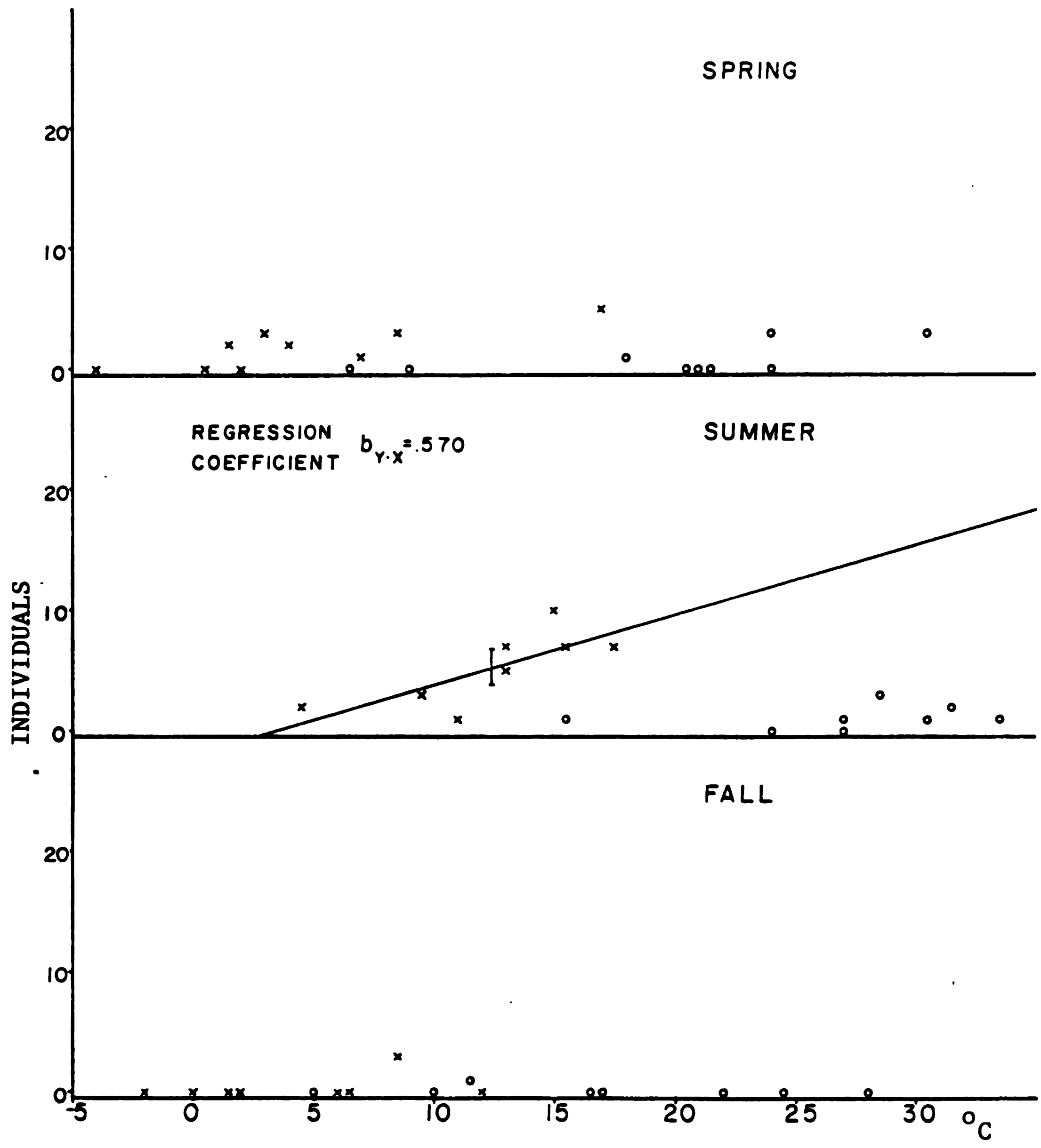


Figure 10. Number of individuals of P. coracinus caught in diel traps in spring, summer and fall, plotted against temperature in °C. Fitted regression lines are drawn where appropriate.

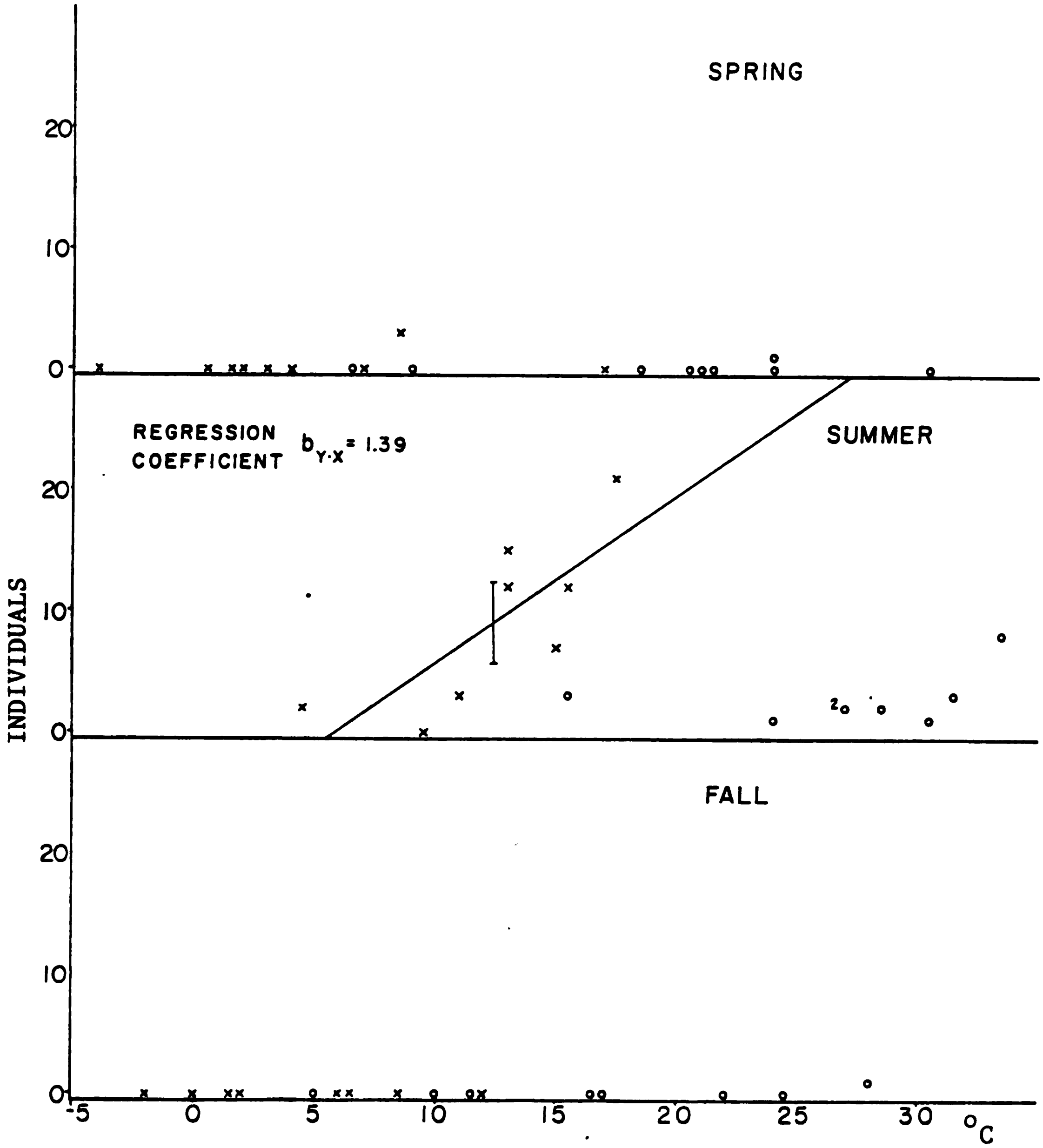


Figure 11. Number of individuals of S. impunctatus caught in diel traps in spring, summer and fall, plotted against temperature in °C. Fitted regression lines are drawn where appropriate.

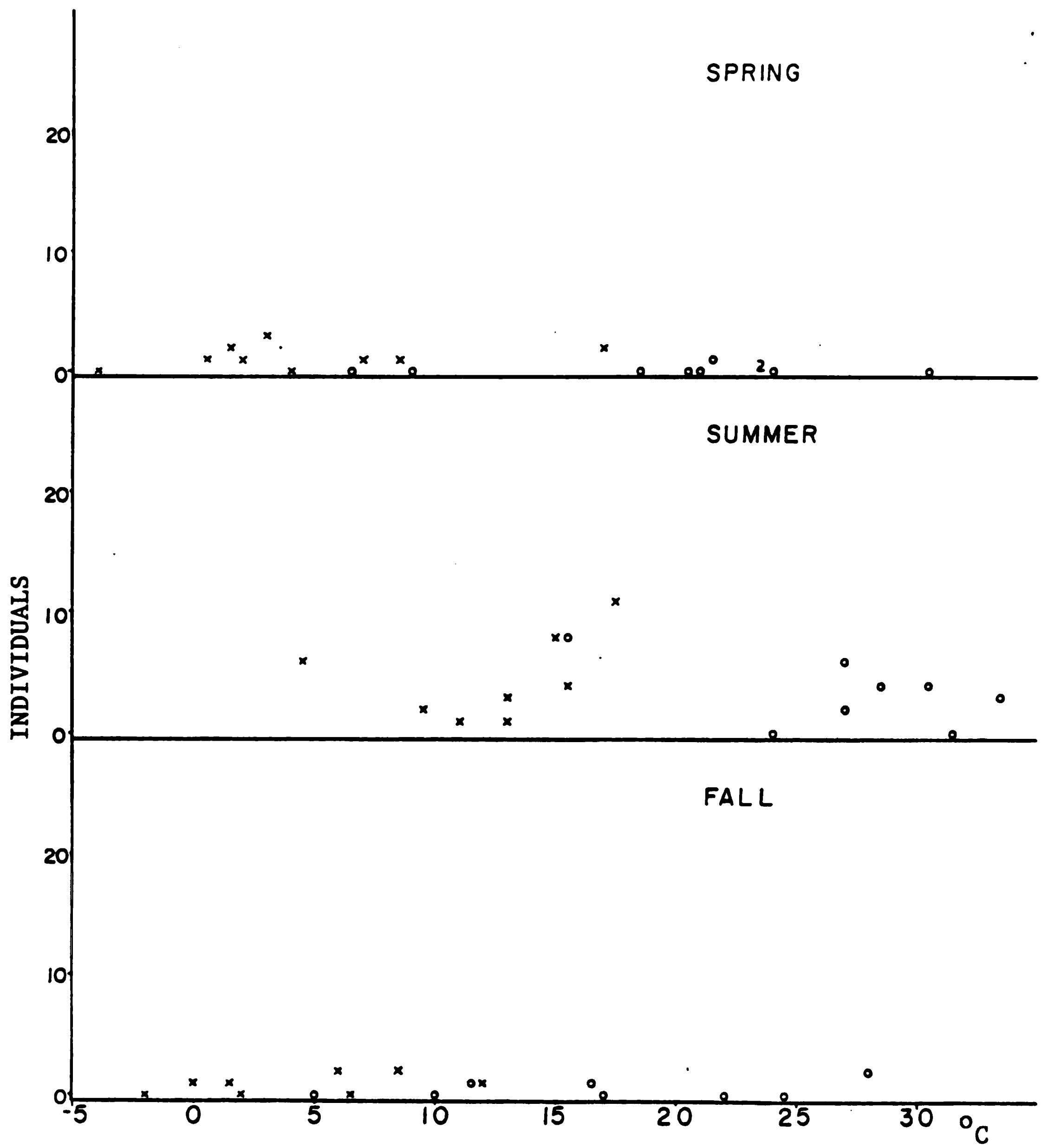


Figure 12. Number of individuals of P. melanarius caught in diel traps in spring, summer and fall, plotted against temperature in °C.

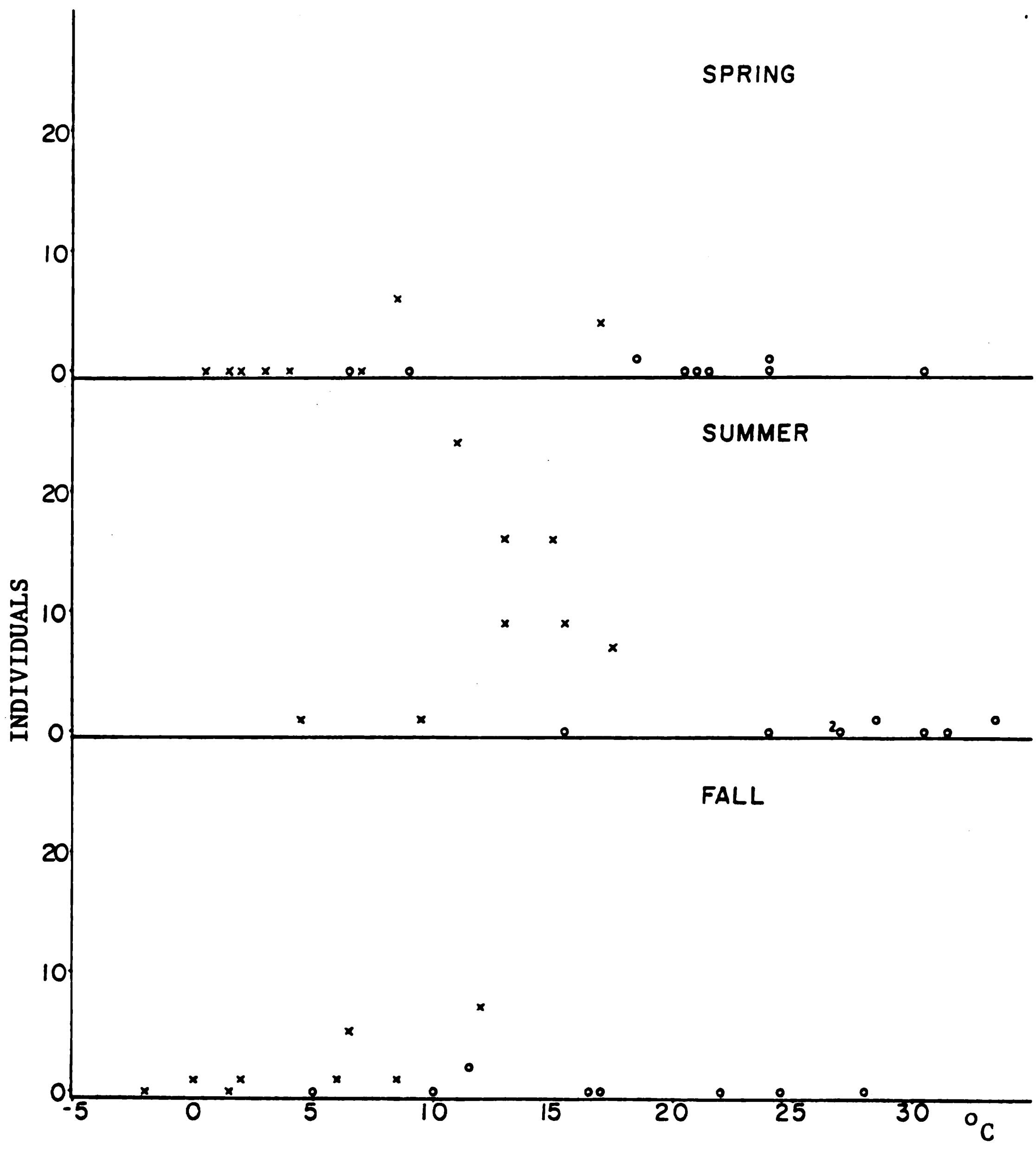


Figure 13. Number of individuals of C. ingratus caught in diel traps in spring, summer and fall, plotted against temperature in °C.

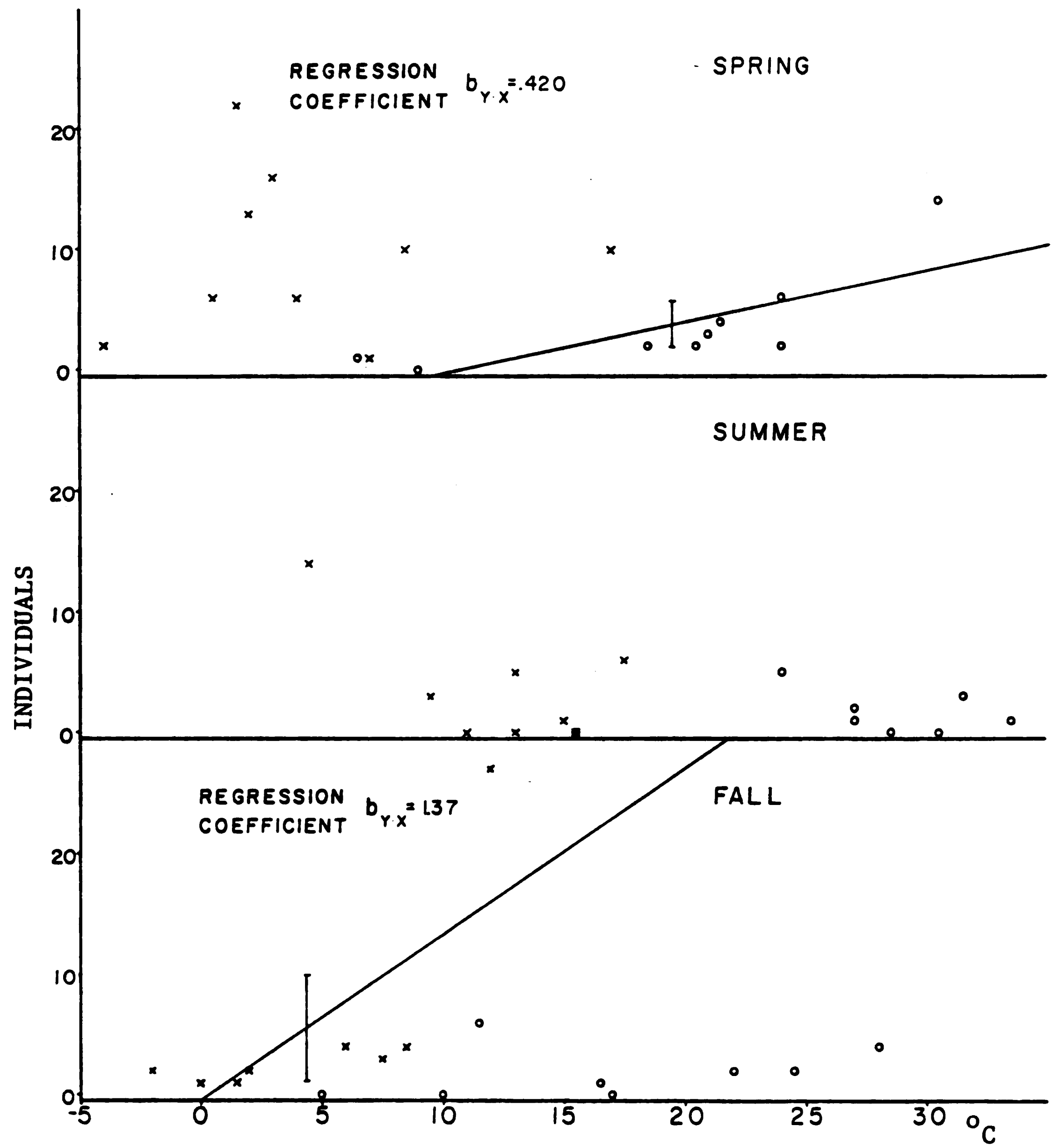


Figure 14. Number of individuals of P. pensylvanicus caught in diel traps in spring, summer and fall, plotted against temperature in °C. Fitted regression lines are drawn where appropriate.

fall peaks, showed a shift in temperature relationships over the course of the season (Figure 14). Spring activity was characterized by day catches significantly increasing with maximum daily temperatures. By contrast, spring night activity had no apparent relationship to temperature. During the fall, on the other hand, night activity increased significantly with minimum temperature and day activity was not associated with daily maximum temperatures. Activity declined during the summer months and did not vary with temperature.

Many authors consider ambient temperature to be a factor regulating activity patterns. Thiele (1977c) stated that temperature was a primary influence affecting diel and annual rhythms. Additionally, Baars (1979), Levesque et al (1979), and Jones (1979) found that warm temperatures were generally associated with high activity levels in several species of carabids.

Results of this study for _P. coracinus_ and _S. impunctatus_ supported findings by Levesque et al (1979) who reported increases in activity in these species at temperatures above 10°C. This study's results for _P. melanarius_, however, contradicted general observations made by Barlow (1970), Levesque et al (1979), and Jones (1979) who reported increased activity in this species with increasing temperatures. Jones (1979) compared _P. melanarius_ activity with accumulated monthly temperatures. Since _P. melanarius_ is a summer breeding species, its activity peak would usually occur when average monthly temperatures were at their highest. Thus, Jones (1979) observation of increased activity during warm months may have been complicated by increased activity in this species induced by breeding. Both Barlow's (1970) and Levesque et al (1979) conclusions were based on simple observations. Neither author tested temperature and activity relationships statistically.

Previous research has shown P. pensylvanicus to be a relatively cold-tolerant species (Goulet, 1974). Levesque et al (1979) reported high activity in this species at temperatures below 5°C. Examination of spring night catches in this study showed high activity levels at nearly freezing temperatures. Yet, fall night activity appeared to be suppressed at cold temperatures, and increased dramatically during one unseasonably warm trapping date. Physiological differences between spring and fall populations may account for this anomaly. The population of P. pensylvanicus adults during autumn, unlike the spring assemblage, was made up of mostly newly-emerged individuals. These individuals may have been unable to tolerate cool temperatures as well as spring adults that have acclimated to cold winter conditions.

Though adults of this species are generally cold-tolerant, warm temperatures are required for reproduction and egg development (Goulet, 1979, Thiele, 1977c). In spring, warm temperatures are often reached only during the day in Michigan's Upper Peninsula. This may explain the positive association between daytime temperatures and diurnal activity during spring, a time when this species is reproductively most active (Barlow, 1970; Goulet, 1974). Activity of reproducing adults may be particularly stimulated by warm temperatures. Indeed, warm day temperatures appeared to induce activity only in breeding adults. No relationship occurred with similar high temperatures during summer and fall.

Dennison and Hodkinson (1983) hypothesized that carabid sensitivity to low temperatures would be reflected in seasonal trends of night and day activity rather than temperature-activity correlations. They found that species in a forest carabid community shifted towards increased diurnalism during early spring and late fall as cool nights inhibited nocturnal activity. Another explanation for this phenomenon is that forest species prefer cool temperatures and restrict any daytime activity to cool days (Thiele, 1979). Inspection of diel activity levels graphed over the trapping season for each species in this study revealed results contrary to both theories (Figures 15-19). Activity declined overall in spring and fall for many species, and almost all diurnal activity occurred during late spring and mid-summer, when both night and day temperatues were at their warmest. Warm temperatures, however, did not appear to directly influence diurnal activity. Except in the case of *P. pensylvanicus* (see above), day activity in carabids in this study showed no association with increasing temperatures. Diel activity in these species is probably regulated by other, more influential factors. Some other possible influences on diel activity are discussed in the next section.

DIEL ACTIVITY

Activity of carabids caught in this study was predominantly nocturnal. Average catch per hour of all carabid species showed an almost five-fold increase in night activity compared to day activity (Table 3). ANOVA statistics showed that influences of night and day activity significantly affected activity in *P. pensylvanicus*, *P. coracinus*, *S. impunctatus*, and *C. ingratus* at $p = .001$ (Table 4).

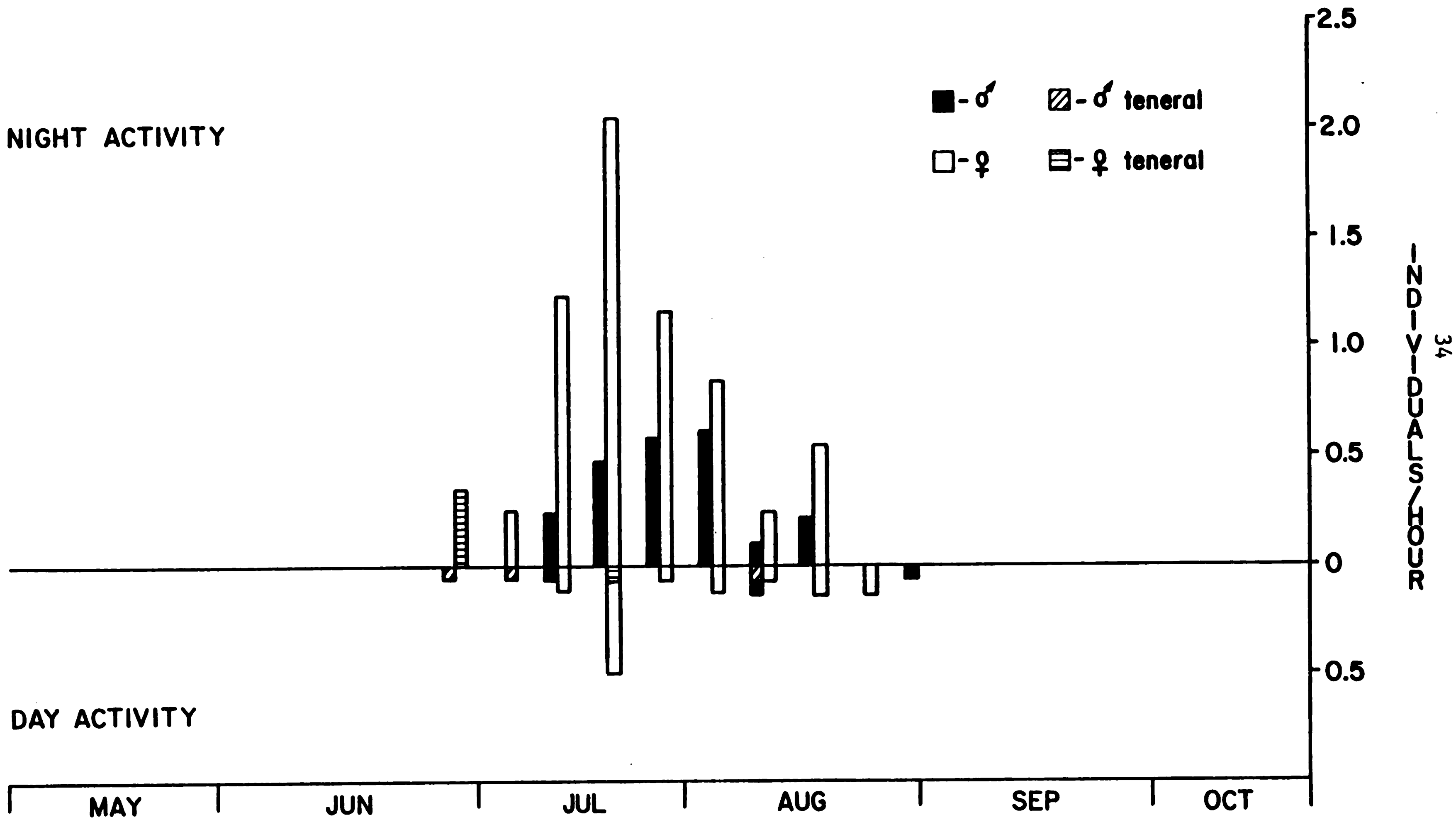


Figure 15. Number of male, female and teneral individuals of S. impunctatus caught per hour at night and during the day for each trapping date.

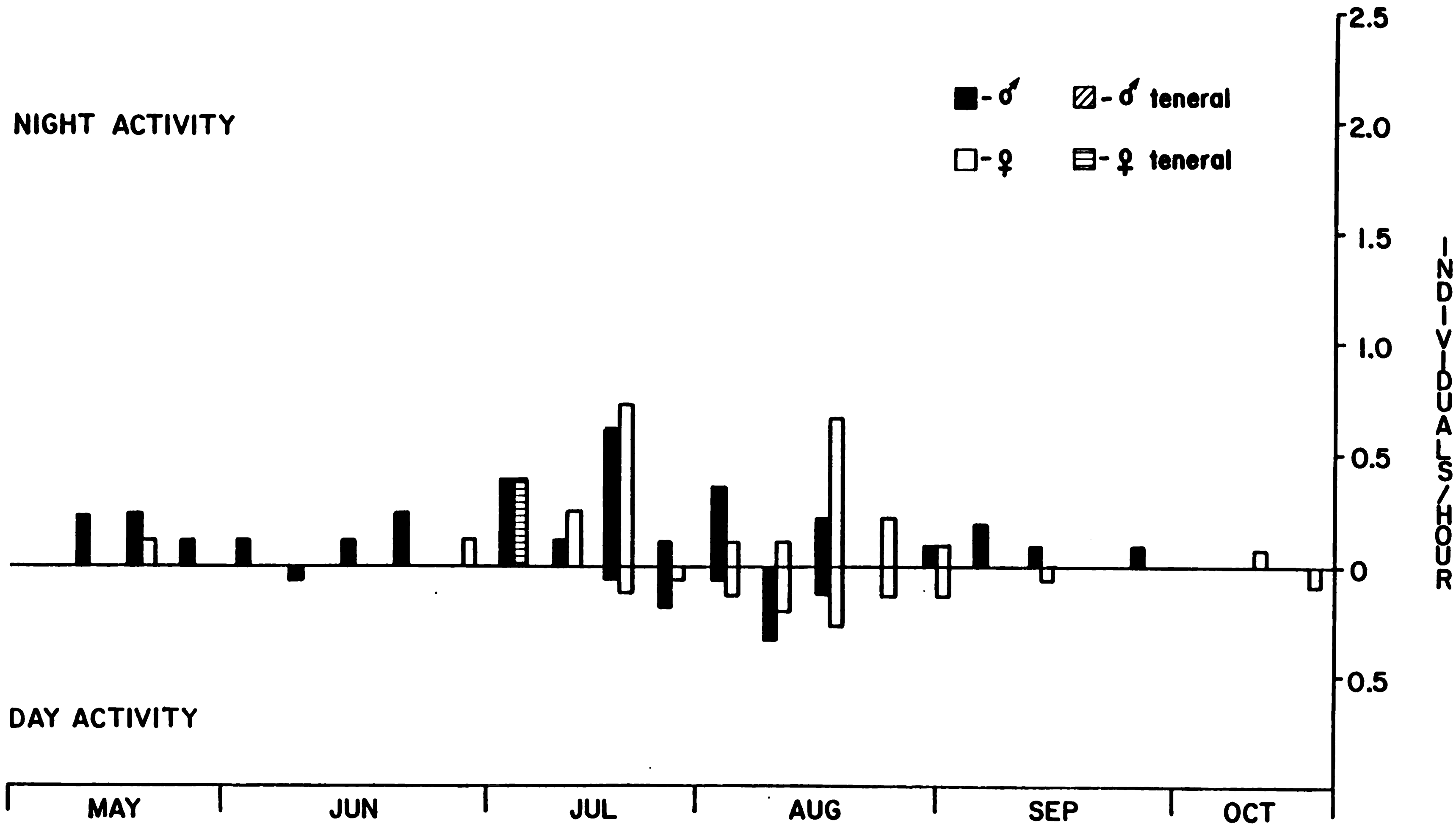


Figure 16. Number of male, female and teneral individuals of P. melanarius caught per hour at night and during the day for each trapping date.

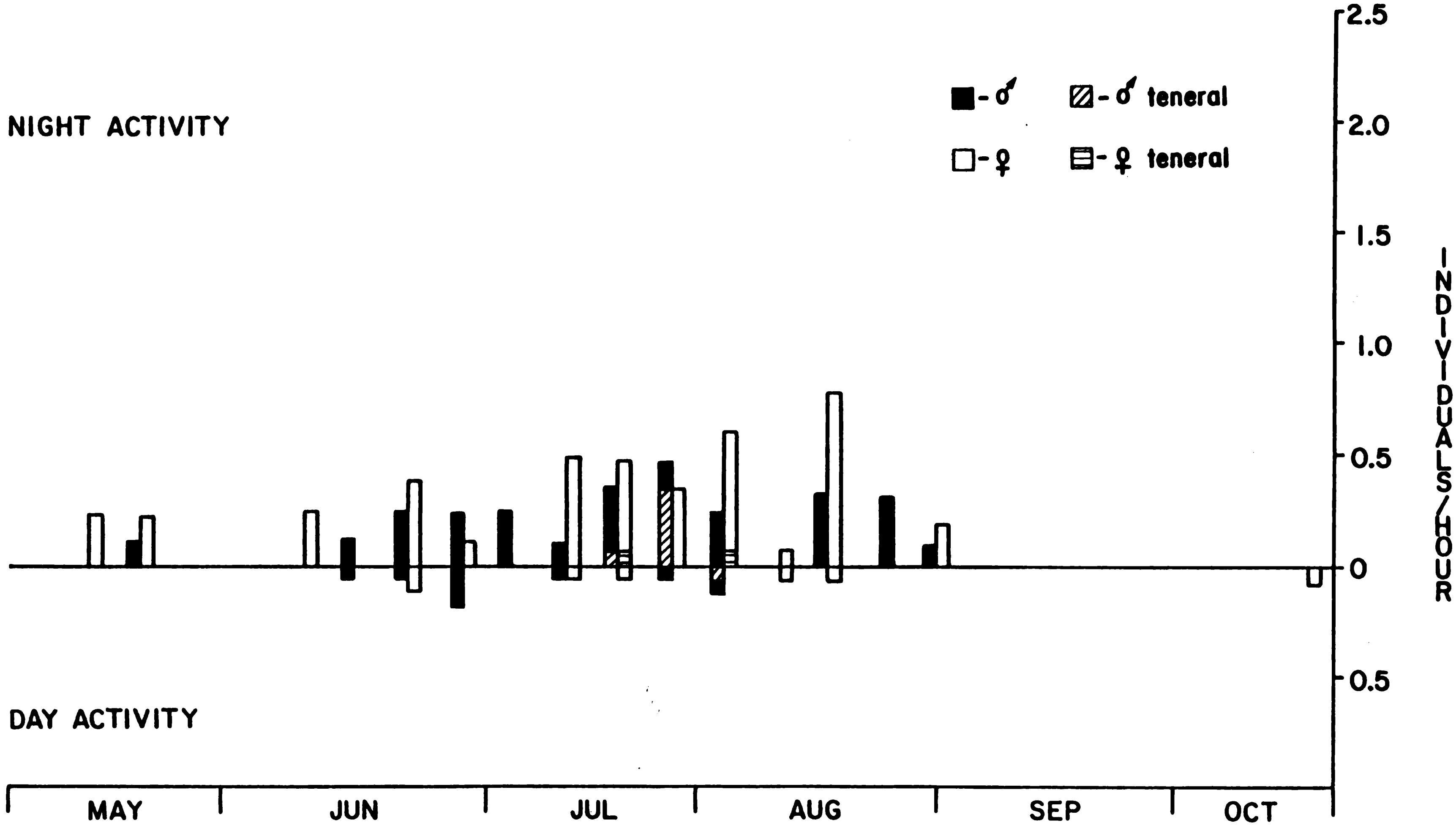


Figure 17. Number of male, female and teneral individuals of <u>P. coracinus</u> caught per hour at night and during the day for each trapping date.

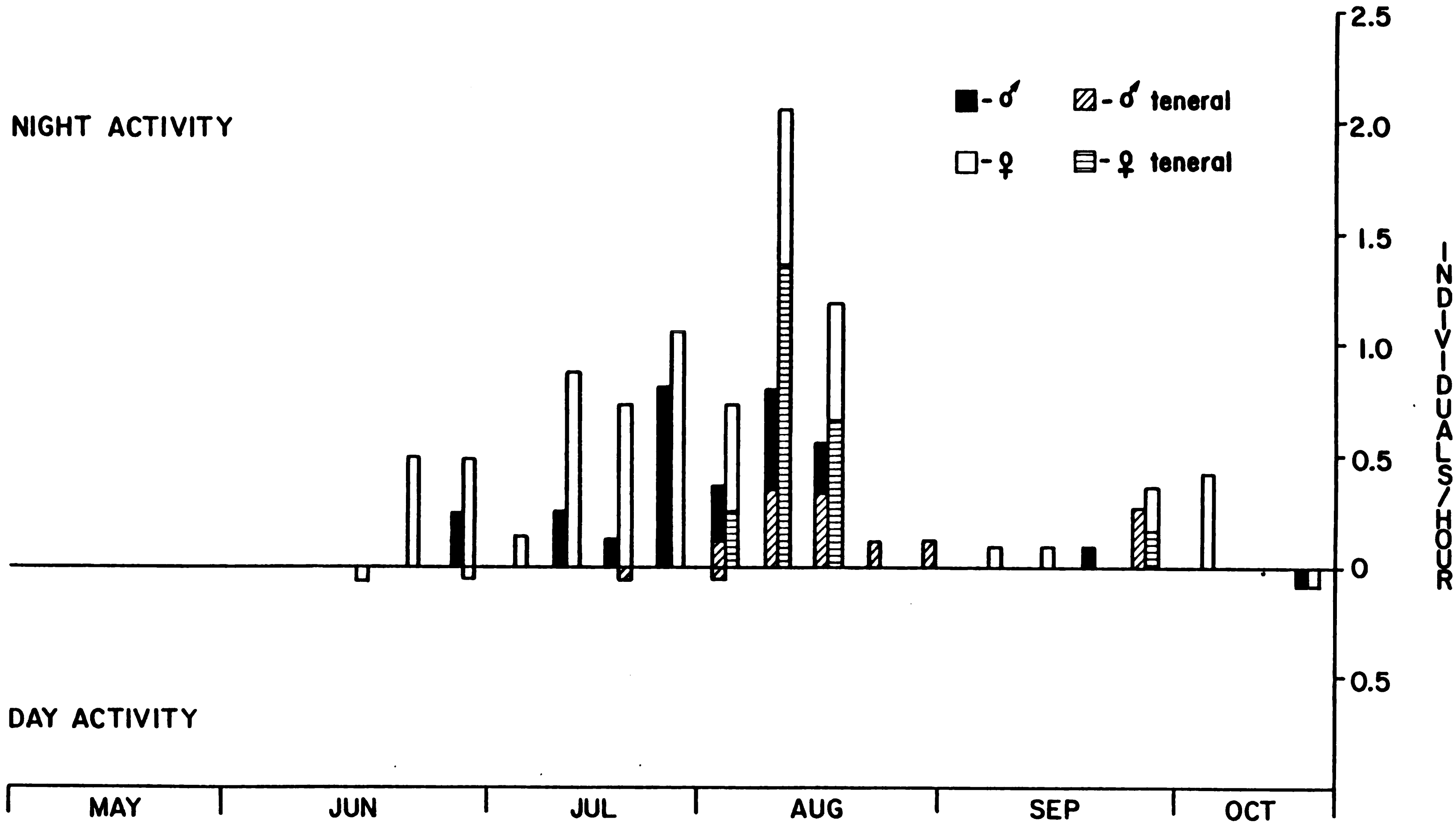


Figure 18. Number of male, female and teneral individuals of C. ingratus caught per hour at night and during the day for each trapping date.

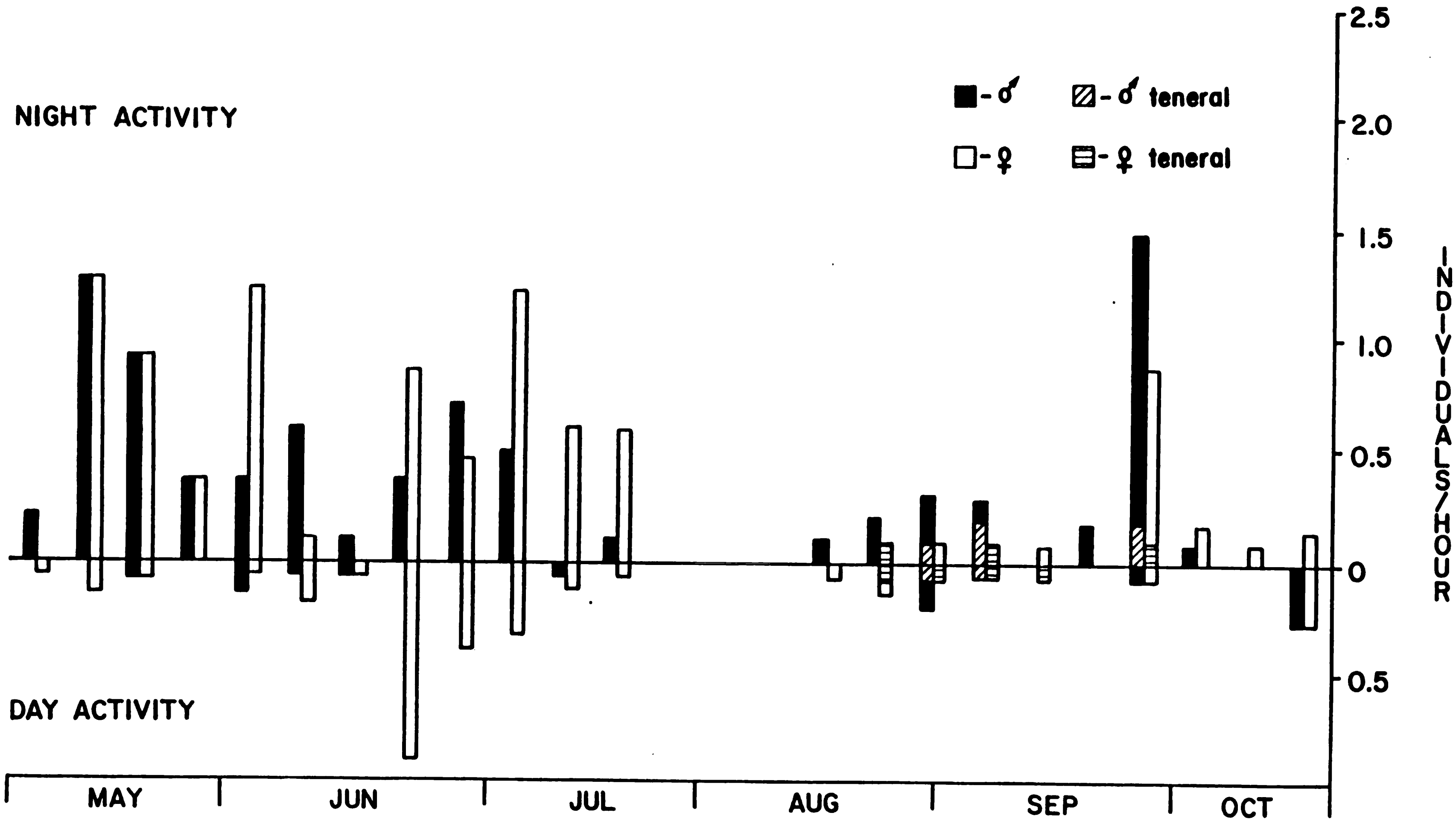


Figure 19. Number of male, female and teneral individuals of P. pensylvanicus caught per hour at night and during the day for each trapping date.

Table 3. Average number of carabids collected per hour at night and during the day for all species and for the 5 most common species at the study site.

species	night catch/hour	day catch/hour
C. ingratus	.49	.02
P. coracinus	.29	.04
P. melanarius	.25	.08
P. pensylvanicus	.72	.19
S. impunctatus	.36	.06
All Carabids	2.34	.49

Table 4. Results of analysis of variance of number of individuals collected per hour by diel factors for the 5 most common species at the research site. Numbers collected per hour were log-transformed. An * denotes accepted significance at $P \leq .001$.

Species	Source of variation	Sum of squares	Degrees of freedom	Mean square	F statistic
P. pensylvanicus	diel	3.093	1	3.093	17.908*
P. melanarius	diel	.137	1	.137	1.863
P. coracinus	diel	1.972	1	1.972	38.150*
S. impunctatus	diel	2.959	1	2.959	34.428*
C. ingratus	diel	2.469	1	2.469	18.303*

The probability that diel effects influenced activity in P. melanarius was 82%. This species was also predominantly night-active, but the difference between night and day activity was not as great as other species exmained (Table 3).

This study's results confirm conclusions reached by previous authors, nocturnal behavior was documented in P. melanarius in European studies (Greenslade, 1963; Luff, 1978; Dennison and Hodkinson, 1983), and was recorded in limited observations of P. coracinus, P. pensylvanicus, and S. impunctatus in eastern Canada (Levesque et al, 1979).

Although carabid activity in this study primarily occurred at night, each species had some incidence of diurnal activity. Levels of this activity varied between species, but except in the case of C. ingratus, a species that showed very little diurnal activity in this study, seasonal occurrences of diurnal activity in the species investigated generally followed their overall seasonal pattern of activity (Figures 15-19). Diurnal activity in these species tended to increase during late spring and summer when their overall activity increased. Diurnal activity in C. ingratus, on the other hand, also occurred near the beginning and end of this species' season of activity (Figure 18).

In field experiments in England, Luff (1978), and Dennison and Hodkinson (1983) found that small carabid species tended to show more diurnal activity than larger species. Their conclusions were based on negative correlations between day activity and mean body size. Luff (1978) suggested that larger species, being more conspicuous during the day, must conceal themselves from predators by hiding deep in litter. Small species, on the other hand, are readily overlooked and can easily find shelter.

In order to test Luff's theory, the product-moment correlation coefficient was calculated for the log of the ratio of mean night and day catches per hour and mean body size for each species. Results refuted Luff's hypothesis (table 5). The correlation coefficient was not significant, but its negative value indicated a trend towards negative correlation between body size and nocturnalism. Notably, _C. ingratus_, the smallest species studied, was the least diurnally active of the five species investigated, and _P. melanarius_, a large species, was the most diurnally active. Luff's (1978) predation theory does not seem to apply in this study.

Many authors theorize that nocturnal species of carabids, especially those in forest habitats, are particularly susceptible to desiccation (Kirk, 1971b; Greenslade, 1965; Thiele and Weber, 1968; and Thiele, 1977c). Restricting their activity to night reduces the exposure of these species to dry conditions since daytime relative humidities are often fairly low, rising only at night (Thiele and Weber, 1968; Bauer, 1977).

Relative humidities in this study, in fact, regularly rose at night and declined substantially during the day (Appendix D). It is suggested that changing humidity levels were a contributing influence on nocturnal activity in the species examined. The tendency in this study towards diurnal activity in _P. melanarius_, a species found in field as well as forests (Lindroth, 1969), may have been due to a greater ability of this species to withstand drier air than the other carabids in this study. Most field species of carabids are adapted to tolerate dry field conditions and hence are not as averse to diurnal activity as forest species (Thiele and Weber, 1968). Additionally, field notes recorded daytime rain during the few isolated instances that C. ingratus was caught in day traps over the season. This species appeared to be active almost solely during periods of high relative humidity and may be particularly sensitive to desiccation.

Table 5. Product-moment correlation statistics of night:day trap collections of the 5 most common carabids investigated and their respective body lengths.

species	log $\frac{\text{average \#/hour-night}}{\text{average \#/hour-day}}$	mean body length (mm)
C. ingratus	1.39	7.7 ± .90
S. impunctatus	.78	9.5 ± .67
P. pensylvanicus	.58	11.5 ± .50
P. coracinus	.86	16.6 ± .80
P. melanarius	.49	17.0 ± .89

Some authors suspect that carabid activity patterns are primarily determined by competition. Williams (1959) and Breymeyer (1966) both postulated that activity of potentially competing ground macrofauna, specifically, carabid beetles, in "older", more evolved communities (e.g., forests) is more symmetrically arranged around a twenty-four hour cycle due to previous competitive interactions than activity in "younger", less evolved communities (e.g., fields) where competition has not yet forced species into different temporal niches. Though the species examined in this study were in an "older" community as defined by Williams (1959), a mature hardwood forest, activity of each species occurred primarily at night, displaying an asymmetrical arrangement of activity. Hence, competition between species did not appear to regulate periodicity in this study.

Intraspecific competition, however, may have operated on some of the carabid species investigated here. Increased diurnal activity in species examined in this study coincided with these species breeding seasons, a time when breeding adults were seeking mates and breeding as well as food (Barlow, 1970). This phenomenon was especially apparent in *P. pensylvanicus*. A comparison of this species spring and fall activity peaks showed that this species was much more day active during spring, its main period of reproduction. Though increased activity may have been stimulated by reproductive factors, competition between individuals of the same species may have also influenced this shift to diurnal activity in the normally nocturnal species of this study.

GENDER EFFECTS

Seasonal and diel activity was found to vary between sexes as well as between species. Comparison of means of males and females caught per trap revealed significant differences in activity between sexes in *P. pensylvanicus*, *S. impunctatus* and *C. ingratus* (Table 7). Females appeared to be more active than males for each

Table 7. Means and standard deviations of males and females caught per trap and results of comparisons using t or q- tests. * denotes accepted significance ($p \leq .05$). The q statistic was used when variances were unequal but coefficients of variation were equal.

Species	Mean	Standard deviation	T or q statistic
P. pensylvanicus			
Overall			
males	5.10	2.49	4.56*
females	8.02	3.19	
spring			
males	2.60	1.70	7.23*
females	4.30	2.37	
fall			
males	1.82	1.51	1.92*
females	1.20	1.36	
P. melanarius			
males	1.55	1.48	.85
females	1.22	1.94	
P. coracinus			
males	1.58	1.34	.38
females	1.70	1.47	
S. impunctatus			
males	2.05	1.96	10.88*
females	4.75	2.89	
C. ingratus			
males	1.55	1.56	10.56*
females	3.60	2.45	

of these species. Admittedly, increased female catches in this study could have been interpreted as greater female density as well as increased female activity. However, it is unlikely that density alone accounted for the disparity between male and female catches because pitfall traps encompass both activity and abundance components in a population. Sex ratios of night and day samples were also compared for each species investigated in this study. Results showed that proportions of females and males significantly differed between night and day for all but one species (table 8). These differences most likely reflected changes in activity between sexes since relative densities of males and females would probably not change appreciably in the course of one day.

Changes in sex ratios indicated that higher levels of female:male activity occurred at night compared to day for P. coracinus, S. impunctatus, and C. ingratus. Ratios of female to male activity increased during the day for P. pensylvanicus rather than at night. Moreover, comparisons of night and day sex ratios during the spring and fall activity peaks of P. pensylvanicus revealed a shift in female activity over the trapping season. Diurnal proportions of females were significantly greater than those of males during the spring for this species, but autumn sex ratios were nearly equal between night and day. This study has shown a positive association between warm day temperatures and diurnal activity of P. pensylvanicus during its spring breeding season. Warm day temperatures may have particularly influenced breeding females in this species. Though adults are cold-tolerant, warmth is important for stimulation of reproduction and egg

Table 8. Means and standard deviations of male:female ratios and results of comparisons between night and day catches using t or q- tests. The q statistic was used when variances were unequal but coefficients of variation were equal.

Species	Mean	Standard deviation	T or q statistic
P. melanarius			
female:male- night	1.17	1.03	.78
female:male- day	1.42	.99	
P. coracinus			
female:male- night	1.75	1.48	4.29*
female:male- day	1.07	.77	
S. impunctatus			
female:male- night	2.34	2.05	5.22*
female:male- day	1.72	.83	
C. ingratus			
female:male- night	1.86	1.20	14.15*
female:male- day	1.12	.39	
P. pensylvanicus			
Overall			
female:male- night	1.25	.67	7.72*
female:male- day	2.26	1.36	
spring			
female:male- night	1.43	1.01	2.16*
female:male- day	2.26	1.39	
fall			
female:male- night	.97	.56	.58
female:male- day	1.08	.60	

development (Goulet, 1974; Thiele, 1977c).

Increased female activity may be related to reproduction in the other species examined in this study. In addition to seeking mates many females must later select specific oviposition sites (Thiele, 1977c). Goulet (1974) found that females of _P. pensylvanicus_ consistently chose the wettest areas of their habitat for oviposition. Although the oviposition habits of _S. impunctatus_, _C. ingratus_, and _P. coracinus_ are poorly known, elaborate nesting behavior has been documented almost solely in the tribe Pterostichini, to which these species belong (Thiele, 1977c). Furthermore, gravid females may need extra nutrition for their developing eggs. Females trapped in this study tended to be larger than their male counterparts.

SUMMARY

Definite seasonal and diel activity patterns were revealed in _P. pensylvanicus_, _P. coracinus_, _P. melanarius_, _S. impunctatus_ and _C. ingratus_ in Michigan's Upper Peninsula. Seasonal patterns displayed by these species corresponded closely to their breeding seasons as documented in the literature. Increases in activity tended to coincide with periods of reproduction.

Temperature was associated with activity in some species investigated. Night activity was positively associated with minimum temperatures in most cases, other species showed little or no response to temperature. _P. pensylvanicus_, in particular, showed a shift in temperature relationships with activity through the trapping season.

Each species was nocturnal. High humidity levels at night may have favored nocturnal activity in the species studied. Varying

amounts of diurnal activity, however, occurred in each species. In most species, this diurnal activity increased during breeding season. Intraspecific competition between breeding adults for mates and breeding areas may have induced diurnal activity in these normally nocturnal species.

Females were more frequently captured than males in this study. Furthermore, activity levels of females varied disproportionately between night and day catches for some species. *P. pensylvanicus*, again, showed seasonal shifts in female:male activity ratios. Increased female activity occurred during breeding seasons for most species investigated. Gravid females seeking food and oviposition sites may have contributed to this increase in activity.

APPENDIX A

Formulae for vegetation analyses

Tree data

Density/100 m^2 = 100 m^2/(average distance in meters)^2

Relative density of species A = $\dfrac{\text{\# of trees of species A encountered}}{\text{\# of trees encountered}}$ X density for all trees

Dominance or Cover = Relative density of species A X Average basal area of species A for species A

Shrub data

Absolute coverage of species A = $\dfrac{\text{total length of transects intercepted by species A}}{\text{total length of transects (20,000 cm)}}$

Relative coverage of species A = $\dfrac{\text{absolute coverage of species A}}{\text{total shrub coverage}}$

Absolute frequency of species A = $\dfrac{\text{\# of transects species A occurs at}}{\text{total \# of transects (20)}}$ X 100

Relative frequency of species A = $\dfrac{\text{absolute frequency of species A}}{\text{sum of absolute frequencies for all species}}$ X 100

Dominance of species A = relative frequence of species A + relative coverage of species A

Herb data

Absolute frequency of species A = $\dfrac{\text{\# of plots species A occurs in}}{\text{total \# of plots}}$ X 100

Relative frequency of species A = $\dfrac{\text{absolute frequency of species A}}{\text{sum total of absolute frequencies}}$ X 100

Absolute cover of species A = Average cover values of species A over 20 plots
Relative cover of species A = Average of relative cover values calculated at each plot

Relative cover of species A per plot = $\dfrac{\text{cover value of species A at plot Y}}{\text{total cover values at plot Y}}$ X 100

Dominance of species A = Relative frequency of species A + Relative cover of species A

APPENDIX B
TRAPPING SCHEDULE

May

ND ND ND ND

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 16 1 1 20 21 22 23 24 25 26 27 28 29 30 31

Jun

ND ND ND ND ND

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

Jul

ND ND ND ND

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31

Aug

ND ND ND ND N

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31

Sep

D ND ND ND ND

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

Oct

ND ND ND

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31

APPENDIX C

Minimum and Maximum temperatures used for regression statistics in °C

date	Maximum daily temperature	Averaged minimum daily temperature
5/May	6.5	-4.0
12/May	24.0	1.5
19/May	20.5	3.0
26/May	9.0	0.5
2/Jun	21.0	2.0
10/Jun	21.5	4.0
17/Jun	18.5	7.0
23/Jun	30.5	17.0
30/Jun	24.0	8.5
7/Jul	24.0	4.5
14/Jul	31.5	13.0
21/Jul	33.5	17.5
28/Jul	30.5	13.0
4/Aug	28.5	15.5
11/Aug	15.5	11.0
18/Aug	27.0	15.0
25/Aug	27.0	9.5
1/Sep	28.0	8.5
8/Sep	22.0	6.0
14/Sep	16.5	0.0
22/Sep	10.0	2.0
29/Sep	24.5	12.0
6/Oct	17.0	6.5
13/Oct	5.0	1.5
27/Oct	11.5	2.0

APPENDIX D

Average night and day relative humidities

date	average R.H.-night	average R.H.-day
26/Aug	96.2%	85.2%
27/Aug	93.5	72.5
28/Aug	93.2	77.7
29/Aug	92.5	83.8
30/Aug	96.8	83.5
31/Aug	93.5	70.0
1/Sep	90.3	73.7
22/Sep	92.0	84.0
23/Sep	90.3	75.8
24/Sep	85.5	68.7
25/Sep	89.2	78.7
26/Sep	88.2	87.7
27/Sep	89.8	85.2

APPENDIX E

Length, in hours, of night and day trapping periods through the season

date	night length	day length
4-5/May	9.25	15.25
11-12/May	8.50	15.00
18-19/May	8.50	15.00
25-26/May	8.00	16.00
1-2/Jun	8.00	15.50
9-10/Jun	8.00	16.00
16-17/Jun	8.25	17.00
22-23/Jun	8.00	16.00
29-30/Jun	8.25	15.50
6-7/Jul	7.75	16.00
13-14/Jul	8.00	16.00
20-21/Jul	8.25	16.00
27-28/Jul	8.50	15.75
3-4/Aug	8.25	15.75
10-11/Aug	8.75	15.00
17-18/Aug	9.00	15.00
24-25/Aug	9.25	14.85
31-Aug/1-Sep	9.75	14.50
7-8/Sep	10.00	13.75
13-14/Sep	10.50	13.50
21-22/Sep	11.25	12.75
28-29/Sep	11.25	12.50
5-6/Oct	12.00	12.00
12-13/Oct	12.50	11.50
26-27/Oct	13.00	11.00

APPENDIX F

NIGHT/DAY SAMPLE DATA

<u>C. ingratus</u>			N			D							
		#/hr		#/hr		#/hr		#/hr	Total N	# N/hr	Tot D	# D/hr	Grand Total
4-5/May	0	0	0	0	0	0	0	0	0	0	0	0	0
11-12/May	0	0	0	0	0	0	0	0	0	0	0	0	0
18-19/May	0	0	0	0	0	0	0	0	0	0	0	0	0
25-26/May	0	0	0	0	0	0	0	0	0	0	0	0	0
1-2/Jun	0	0	0	0	0	0	0	0	0	0	0	0	0
9-10/Jun	0	0	0	0	0	0	0	0	0	0	0	0	0
16-17/Jun	0	0	0	0	0	0	1	.06	0	0	1	.06	1
22-23/Jun	0	0	4	.50	0	0	0	0	4	.50	0	0	4
29-30/Jun	2	.24	4	.48	0	0	1	.06	6	.73	1	.06	7
6-7/Jul	0	0	1	.13	0	0	0	0	1	.13	0	0	1
13-14/Jul	2	.25	7	.88	0	0	0	0	9	1.12	0	0	9
20-21/Jul	1	.12	6	.73	0	0	1	.06	7	.85	1	.06	8
27-28/Jul	7	.82	9	1.06	0	0	0	0	16	1.88	0	0	16
3-4/Aug	3	.36	6	.73	1	.06	0	0	9	1.09	1	.06	10
10-11/Aug	7	.80	17	2.06	0	0	0	0	24	2.74	0	0	24
17-18/Aug	5	.56	11	1.2	0	0	0	0	16	1.78	0	0	16
24-25/Aug	1	.11	0	0	0	0	0	0	1	.11	0	0	1
31-Aug/1-Sep	1	.10	0	0	0	0	0	0	1	.10	0	0	1
7-8/Sep	0	0	1	.10	0	0	0	0	1	.10	0	0	1
13-14/Sep	0	0	1	0	0	0	0	0	1	.10	0	0	1
21-22/Sep	1	.04	0	.36	0	0	0	0	1	.09	0	0	1
28-29/Sep	3	.27	4	.42	0	0	0	0	7	.62	0	0	7
5-6/Oct	0	0	5	0	0	0	0	0	5	.42	0	0	5
12-13/Oct	0	0	0	0	0	0	0	0	0	0	0	0	0
26-27/Oct	0	0	0		1	.09	1	.09	0	0	2	.18	2
TOTALS	33		76		2		4		109		6		115

NIGHT/DAY SAMPLE DATA

P. coracinus			N				D						
		# / hr		# / hr		# / hr		# / hr	Total N	# N / hr	Tot D	# D / hr	Grand Total
4-5/May	0	0	0	0	0	0	0	0	0	0	0	0	0
11-12/May	0	0	2	0.23	0	0	0	0	2	0.23	0	0	2
18-19/May	1	0.12	2	0.23	0	0	0	0	3	0.35	0	0	3
25-26/May	0	0	0	0	0	0	0	0	0	0	0	0	0
1-2/Jun	0	0	0	0	0	0	0	0	0	0	0	0	0
9-10/Jun	0	0	2	0.25	0	0	0	0	2	0.25	0	0	2
16-17/Jun	1	0.12	0	0	1	0.06	0	0	1	0.12	1	0.06	2
22-23/Jun	2	0.25	3	0.38	1	0.06	2	0.12	5	0.62	3	0.19	8
29-30/Jun	2	0.24	1	0.12	3	0.19	0	0	3	0.36	3	0.19	6
6-7/Jul	2	0.26	0	0	0	0	0	0	2	0.26	0	0	2
13-14/Jul	1	0.12	4	0.50	1	0.06	1	0.06	5	0.62	2	0.12	7
20-21/Jul	3	0.36	4	0.48	0	0	1	0.06	7	0.85	1	0.06	8
27-28/Jul	4	0.47	3	0.35	1	0.06	0	0	7	0.92	1	0.06	8
3-4/Aug	2	0.24	5	0.61	3	0.13	0	0	7	0.85	2	0.13	9
10-11/Aug	0	0	1	0.11	0	0	1	0.07	1	0.11	1	0.07	2
17-18/Aug	3	0.33	7	0.78	0	0	1	0.07	10	1.11	1	0.07	11
24-25/Aug	0	0	3	0.32	0	0	0	0	3	0.32	0	0	3
31-Aug/1-Sep	1	0.10	2	0.20	0	0	0	0	3	0.31	0	0	3
7-8/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
13-14/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
21-22/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
28-29/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
5-6/Oct	0	0	0	0	0	0	0	0	0	0	0	0	0
12-13/Oct	0	0	0	0	0	0	0	0	0	0	0	0	0
26-27/Oct	0	0	0	0	0	0	1	0.09	0	1	1	0.09	1
TOTALS	22		39		10		7		61		17		

NIGHT/DAY SAMPLE DATA

<u>*P. melanarius*</u>		N				D							
		#/hr		#/hr		#/hr		#/hr	Total N	# N/hr	Tot D	# D/hr	Grand Total
4-5/May	0	0	0	0	0	0	0	0	0	0	0	0	0
11-12/May	2	0.23	0	0	0	0	0	0	2	0.23	0	0	2
18-19/May	2	0.23	1	0.12	0	0	0	0	3	0.35	0	0	3
25-26/May	0	0	1	0.12	0	0	0	0	1	0.12	0	0	1
1-2/Jun	0	0	1	0.12	0	0	0	0	1	0.12	0	0	1
9-10/Jun	0	0	0	0	1	0.06	0	0	0	0	1	0.06	1
16-17/Jun	1	0.12	0	0	0	0	0	0	1	0.12	0	0	1
22-23/Jun	2	0.25	0	0	0	0	0	0	2	0.25	0	0	2
29-30/Jun	1	0.12	1	0.12	0	0	0	0	2	0.24	0	0	2
6-7/Jul	3	0.39	3	0.39	0	0	0	0	6	0.77	0	0	6
13-14/Jul	1	0.12	2	0.25	0	0	0	0	3	0.37	0	0	3
20-21/Jul	5	0.61	6	0.73	1	0.06	2	0.12	11	1.33	3	0.19	14
27-28/Jul	1	0.12	0	0	3	0.19	1	0.06	1	0.12	4	0.25	5
3-4/Aug	3	0.36	1	0.12	1	0.06	3	0.19	4	0.48	4	0.25	8
10-11/Aug	0	0	1	0.11	5	0.33	3	0.2	1	0.11	8	0.53	9
17-18/Aug	2	0.22	6	0.67	2	0.13	4	0.27	8	0.89	6	0.40	14
24-25/Aug	1	0.11	1	0.11	0	0	2	0.14	2	0.22	2	0.13	4
31-Aug/1-Sep	1	0.10	1	0.10	0	0	2	0.14	2	0.20	2	0.14	4
7-8/Sep	2	0.20	0	0	0	0	0	0	2	0.20	0	0	2
13-14/Sep	1	0.09	0	0	0	0	1	0.07	1	0.09	1	0.07	2
21-22/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
28-29/Sep	1	0.09	0	0	0	0	0	0	1	0.09	0	0	1
5-6/Oct	0	0	0	0	0	0	0	0	0	0	0	0	0
12-13/Oct	0	0	1	0.08	0	0	0	0	1	0.08	0	0	1
26-27/Oct	0	0	1	0	0	0	1	0.09	0	0	1	0.09	1
TOTALS	29		26		13		19		55		32		88

NIGHT/DAY SAMPLE DATA

<u>S. impunctatus</u>	N				D								
		#/hr		#/hr		#/hr		#/hr	Total N	# N/hr	Tot D	# D/hr	Grand Total
4-5/May	0	0	0	0	0	0	0	0	0	0	0	0	0
11-12/May	0	0	0	0	0	0	0	0	0	0	0	0	0
18-19/May	0	0	0	0	0	0	0	0	0	0	0	0	0
25-26/May	0	0	0	0	0	0	0	0	0	0	0	0	0
1-2/Jun	0	0	0	0	0	0	0	0	0	0	0	0	0
9-10/Jun	0	0	0	0	0	0	0	0	0	0	0	0	0
16-17/Jun	0	0	0	0	0	0	0	0	0	0	0	0	0
22-23/Jun	0	0	0	0	0	0	0	0	0	0	0	0	0
29-30/Jun	0	0	3	0.36	1	0.06	0	0	3	0.36	1	0.06	4
6-7/Jul	0	0	2	0.26	0	0	1	0.06	2	0.26	1	0.06	3
13-14/Jul	2	0.25	10	1.25	1	0.06	2	0.12	12	1.50	3	0.19	15
20-21/Jul	4	0.48	17	2.06	0	0	8	0.5	21	2.54	8	0.50	29
27-28/Jul	5	0.59	10	1.18	0	0	1	0.06	15	1.76	1	0.06	16
3-4/Aug	5	0.61	7	0.85	0	0	2	0.13	12	1.45	2	0.13	14
10-11/Aug	1	0.11	2	0.23	2	0.13	1	0.07	3	0.34	3	0.20	6
17-18/Aug	2	0.22	5	0.56	0	0	2	0.13	7	0.78	2	0.13	9
24-25/Aug	0	0	0	0	0	0	2	0.14	0	0	2	0.13	2
31-Aug/1-Sep	0	0	0	0	1	0.07	0	0	0	0	1	0.07	1
7-8/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
13-14/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
21-22/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
28-29/Sep	0	0	0	0	0	0	0	0	0	0	0	0	0
5-6/Oct	0	0	0	0	0	0	0	0	0	0	0	0	0
12-13/Oct	0	0	0	0	0	0	0	0	0	0	0	0	0
26-27/Oct	0	0	0	0	0	0	0	0	0	0	0	0	0
TOTALS	19		56		5		19		75		24		99

APPENDIX F

24 Hour Trap Catches

	C. ingratus			*P. coracinus*			*P. melanarius*		
			Total			Total			Total
4-5/May	0	0	0	0	0	0	0	0	0
11-12/May	0	0	0	0	0	0	0	0	0
18-19/May	0	0	0	1	1	2	0	0	0
25-26/May	0	0	0	0	0	0	0	0	0
1-2/Jun	0	0	0	0	3	3	0	0	0
9-10/Jun	0	0	0	1	0	1	0	0	0
16-17/Jun	0	0	0	0	1	1	0	0	0
22-23/Jun	1	3	4	2	1	3	0	0	0
29-30/Jun	5	1	6	5	3	8	0	2	2
6-7/Jul	7	1	8	1	2	3	0	2	2
13-14/Jul	10	1	11	3	3	6	0	2	2
20-21/Jul	5	2	7	0	4	4	0	3	3
27-28/Jul	2	1	3	2	2	4	0	0	0
3-4/Aug	0	3	3	0	4	4	0	3	3
10-11/Aug	8	4	12	2	1	3	1	1	2
17-18/Aug	11	1	12	1	3	4	1	5	6
24-25/Aug	3	1	4	3	3	6	0	2	2
31-Aug/1-Sep	1	1	2	1	0	1	0	0	0
7-8/Sep	0	0	0	0	0	0	0	0	0
13-14/Sep	1	1	2	0	0	0	0	0	0
21-22/Sep	0	1	1	0	0	0	0	0	0
28-29/Sep	6	3	9	0	0	0	0	0	0
5-6/Oct	1	1	2	0	0	0	0	0	0
12-13/Oct	1	0	1	0	0	0	0	0	0
26-27/Oct	2	2	4	0	0	0	0	0	0
TOTALS	64	27	91	22	31	53	2	20	22

24 Hour Trap Catches

	P. pensylvanicus			*S. impunctatus*		
			Total			Total
4-5/May	0	0	0	0	0	0
11-12/May	17	11	28	0	0	0
18-19/May	5	7	12	0	0	0
25-26/May	4	3	7	0	0	0
1-2/Jun	21	16	37	0	0	0
9-10/Jun	10	10	20	0	0	0
16-17/Jun	9	0	9	0	0	0
22-23/Jun	23	5	28	1	1	2
29-30/Jun	12	7	19	5	2	7
6-7/Jul	14	4	18	7	0	7
13-14/Jul	31	10	41	26	4	30
20-21/Jul	15	2	17	24	11	35
27-28/Jul	0	0	0	26	14	40
3-4/Aug	1	0	1	11	8	19
10-11/Aug	0	1	1	4	8	12
17-18/Aug	2	0	2	8	9	17
24-25/Aug	1	1	2	3	0	3
31-Aug/1-Sep	0	1	1	0	0	0
7-8/Sep	4	6	10	0	1	1
13-14/Sep	6	3	9	0	0	0
21-22/Sep	3	2	5	0	0	0
28-29/Sep	7	14	21	0	0	0
5-6/Oct	1	4	5	0	0	0
12-13/Oct	1	4	5	0	0	0
26-27/Oct	3	5	8	0	0	0
TOTALS	190	116	306	115	58	173

LITERATURE CITED

Adis, J. 1979. Problems of interpreting arthropod sampling with pitfall traps. Zool. Anz., 202:177-184.

Andrews, A. W. 1921. The Coleoptera of the Shiras expedition to Whitefish Point, Chippewa County, Michigan. Mi. Acad. Sci. Arts, Let., Papers, 1:293-390.

Baars, M. A., 1979. Patterns of movement of radioactive Carabid Beetles. Oecologia, 44:125-140.

Barlow, C. A. 1970. Phenology and distribution of some Pterostichus of Eastern Canada. J. N.Y. Ent. Soc., 78:215-236.

Bauer, Thomas. 1977. The relevance of the brightness to visual acuity, predation, and activity of visually hunting ground-beetles (Coleoptera, Carabidae). Oecologia, 30:63-73.

Beck, S. D. 1980. Insect Photoperiodism, 2nd Ed. Academic Press, Toronto. 387 pp.

Boiteau, G. 1983. Activity and distribution of Carabidae, Arachnida, and Staphylinidae in New Brunswick potato fields. Can. Ent., 115:1023-1030.

Boucher, J. F. and J. C. Malausa. 1984. Daily activity of young adult micropopulations of Chrysocarabus olympiae Sella (Coleoptera, Carabidae) (in French). Rev. Ecol. Biol. Sol., 21(1):77-86.

Breymeyer, A. 1966a. Relations between wandering spiders and other epigeic predatory arthropoda. Ekol. Polska. A., 14:1-71.

Breymeyer, A. 1966b. Diurnal cycles of the macrofauna in age-different biocoenoses. Pols. Akad. Nauk Bull. Ser. D Sci. Biol., 14:211-213.

Briggs, J. B. 1961. A comparison of pitfall trapping and soil sampling in assessing populations of two species of Carabidae. East Malling Res. Sta. Ann. Report, 108-112.

Brower, J. H. and J. L. Zar. 1977. Field and Laboratory Methods for general Ecology. Wm. C. Brown, Dubuque, Iowa. 194 pp.

Calhoun, J. B. 1944. Twenty-four hour periodicities in the animal kingdom. Pt.I. Journal of the Tenn. Acad. Sci., 19 # 2 & 3, pp. 179-262.

Dennison, D. F. and I. D. Hodkinson. 1983. Structure of the predatory beetle community in a woodland soil ecosystem. II. Diurnal Activity Rhythms. Pedobiologia, 25:169-174.

Dennison, D. F. and Hodkinson, I. D. 1984a. Structure of the predatory beetle community in a woodland soil ecosystem. III. Seasonal activity patterns as revealed by pitfall trapping. Pedobiologia, 26:45-56.

Dennison, D. F. and I. D. Hodkinson. 1984b. Structure of the predatory beetle community in a woodland soil ecosystem. IV. Population Densities and Community Composition. Pedobiologia, 26:157-170.

Desender, K. 1983. Ecological data on Clivina fossor from a pasture ecosystem. Pedobiologia, 25:157-167.

Desender, K., J. P. Maelfait, M. D'Hulster and L. Vanhercke. 1981. Ecological and faunal studies on Coleoptera in agricultural land. I. Seasonal occurrence of Carabidae in the grassy edge of a pasture. Pedobiologia, 22:379-384.

Desender, K. and J. P. Maelfait. 1983. Population restoration by means of dispersal, studies for different carabid beetles in a pasture ecosystem. In New Trends in Soil Biology. Proc. VII International Coll. Soil Zoology. Belgium. 1982 ed. Lebrun.

Dondale, C. D., J. H. Redner and R. B. Semple. 1972. Diel activity periodicities in meadow Arthropods. Can. J. Zool., 50:1155-1163.

Dorr, J. A. and D. F. Eschman. 1970. Geology of Michigan. University of Michigan Press. Ann Arbor, MI. 476 pp.

Ericson, D. 1977. Estimating population parameters of Pterostichus cupreus and P. melanarius in arable fields by means of capture-recapture. Oikos, 29:407-417.

Goulet, H. 1974. Biology and relationships of Pterostichus adstrictus and P. pensylvanicus. Quast. Ent. 10:3-33.

Greenslade, P. J. M. 1963. Daily rhythms of locomotor activity in some Carabidae (Coleoptera). Ent. Exp. and Appl., 6:17-80.

Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). J. Anim. Ecol., 33:301-310.

Greenslade, P. J. M. 1965. On the ecology of some British Carabid beetles with especial reference to life histories. Trans. Soc. Brit. Ent., 16:149-177.

Grum, L. 1966. Diurnal activity rhythm of starved Carabidae. Bull. Acad. Polon. Sci., ClII, 14(6):405-411.

Hubbard, H. G. and E. A. Schwarz. 1878. The Coleoptera of Michigan. Amer. Phil. Soc. Proc., 17:593-666.

Johnson, N. E., Lawrence, W. H. and I. D. Ellis. 1966. Seasonal occurrence of ground beetles in three habitats in southwestern Washington. Annals Ent. Soc. Amer., 59(6):1055-1059.

Jones, M. G. 1979. The abundance and reproductive activity of common Carabidae in a winter wheat crop. Ecol. Ent., 4(1):31-43.

Joosse, E. N. G. and J. M. Kapteijn. 1968. Activity-stimulating phenomena caused by field disturbance in the use of pitfall traps. Oecologia, 1:385-392.

Kirk, V. M. 1971a. Ground beetles in cropland in South Dakota. Annals Ent. Soc. Amer., 64(1):238-241.

Kirk, V. M. 1971b. Biological studies of a ground beetle, Pterostichus lucublandus. Annals Ent. Soc. Amer., 64(3):540-544.

Krumbiegel, I., 1932. Untersuchungen uber Physiologische Rassenbildung. Zool. Jahrb., Abt. Syst., 63:183-280.

Larsson, S. G. 1939. Entwicklunstypen und Entwicklungszeiten der Danischen Carabiden. Ent. Medd., 20:18-560.

Levesque, C., J. G. Pilon and J. Dube. 1979. Phenologie et activite locomotrice de Coleopteres Carabidae des Laurentides (Quebec). Naturaliste Canadien, 106:355-368.

Lindroth, C. H., 1949. Die Fennoskandischen Carabidae III. Kungl. Vetensk. Handl. B4, 3:1-911.

Lindroth, C. H., 1969. The Ground-Beetles of Canada and Alaska. Opuscula Entomologica, Suppl. (20,24,29,33,34,35). Lund, Sweden.

Luff, M. L. 1978. Diel activity patterns of some field Carabidae. Ecol. Ent., 3:53-62.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and methods of vegetation ecology. John C. Wiley and Sons, New York. 547 pp.

Paarman, W. 1979. Ideas about the evolution of the various annual reproduction rhythms in Carabid beetles of the different climatic zones. In: On the Evolution of Behavior in Carabid Beetles. eds. P. J. DenBoer, H. U. Thiele, and F. Weber. H. Veenman and Zonen bv-Wageningen. 222 pp.

Park, O. and J. G. Keller. 1932. Studies in nocturnal ecology, II. Preliminary analysis of activity rhythms in nocturnal forest insects. Ecology, 13:335-346.

Santer, R. A. 1977. Michigan:Heart of the Great Lakes. Kendall-Hunt. Dubuque, Iowa. 364 pp.

Saunders, D. S. 1982. Insect Clocks, 2nd Ed. Pergamon Press, Toronto. 409 pp.

Smith, R. L. 1966. Ecology and Field Biology. Harper and Row, New York. 686 pp.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. 2nd ed. Freeman and Co., San Francisco. 859 pp.

Stubbe, A., K. Schneider and F. Tietze. 1984. Diurnal activity of some carabid species in pine forests of the dubener Heide G.D.R. (in German). Pedobiologia, 26(2):117-130.

Thiele, H. U. 1977a. Measurement of day-length as a basis for photoperiodism and annual periodicity in the Carabid beetle _Pterostichus nigrita_ F. Oecologia, 30:331-348.

Thiele, H. U. 1977b. Differences in measurement of day-length and photoperiodism in two stocks from subarctic and temperate climates in the Carabid beetle _Pterostichus nigrita_ F. Oecologia, 30:349-365.

Thiele, H. U. 1977c. Carabid beetles in their environment. Zoophysiology and Ecology, v. 10. Springer-Verlag, New York. 369 pp.

Thiele, H. U. 1979. Relationships between annual and daily rhythms, climatic demands and habitat selection in Carabid beetles. _In_: Carabid Beetles:their Evolution, Natural History, and Classification. Ed., Erwin, T. L, G. E. Ball, D. R. Whitehead. Coor. Ed., A. L. Halpern. Dr. W. Junk bv. Boston. 1979. 635 pp.

Thiele, H. U. and F. Weber. 1968. The diurnal activity of Carabid beetles. (in German) Oecologia, 1:315-355.

Uetz, G. and J. D. Unzicker. 1976. Pitfall trapping in ecological studies of wandering spiders. J. Arachnol., 3:101-111.

Williams, G. 1959. Seasonal and diurnal activity of Carabidae, with particular reference to _Nebria_, _Notophilus_, and _Feronia_. Jour. Anim. Ecol., 28:309-330.