AN ABSTRACT OF THE THESIS OF

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Title: PREY CONSUMPTION, SURVIVORSHIP AND OVIPOSITION BY ADULTS OF THE
BARK BEETLE PREDATOR THANASIMUS DUBIUS FABRICIUS (COLEOPTERA:CLERIDAE)

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Abstract approved: _____
William P. Nagel

Laboratory studies were conducted to evaluate the effects of prey
availability on prey consumption, survivorship and oviposition of the
southern pine beetle predator, Thanasimus dubius Fabricius. Although
prey consumption rates were significantly affected by the sex, size and
ovipositional status of the predator, it was found through correlation
analyses that predator longevity was largely determined by the availability of prey. Predator age was not found to significantly affect
prey consumption rates. Oviposition increased directly with prey consumption to an asymptote determined by the feeding and/or ovipositional
capacity of the predator. Measurements of field populations of predator
and prey under epidemic conditions suggested that predator populations
are not large enough to prevent infestation and killing of susceptible
trees.

Prey Consumption, Survivorship and Oviposition by Adults of the
Bark Beetle Predator Thanasimus dubius Fabricius
(Coleoptera:Cleridae)

by

Robert Harold Turnbow, Jr.

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ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

LIST OF TABLES

Prey Consumption, Survivorship and Oviposition by Adults of the Bark
Beetle Predator Thanasimus dubius Fabricius (Coleoptera:Cleridae)

INTRODUCTION

The clerid beetle Thanasimus dubius Fabricius has long been
recognized as a predator of southern bark beetles (Hopkins, 1893 and
1899). Thatcher and Pickard (1966) have studied the biology of the
clerid in east Texas and Mignot and Anderson (1969) have reviewed the
bionomics of the beetle in North Carolina. Although found in associa-
tion with a large number of bark beetle species, the clerid seems to
be primarily associated with the southern pine beetle, Dendroctonus
frontalis Zimmerman, and the effects of predation by the clerid are
thought to be greatest on that species (Anonymous, 1972).

Dendroctonus frontalis is one of the most destructive insects
of pine in the South (Dixon and Osgood, 1961), attacking most species
of pine within its range. Outbreaks may develop in a wide variety of
stands and sites (Thatcher, 1960). The beetle attacks pines of all
sizes with trees as small as 3/4 inch d.b.h. having been reported
killed (Dixon and Osgood, 1961). Epidemics of the beetle caused ex-
tensive tree mortality throughout the South during the years 1920,
1922-24, 1929-32 and 1949-63 (King, 1972). An epidemic which began
in 1971 had by 1973 involved some 47 million acres of pine type in
ten southern states and losses of sawtimber alone for 1973 were
predicted to exceed 580 million board feet (Kucera and Barry, 1973).

Large and sudden population fluctuations characterize the

southern pine beetle (Thatcher, 1960). Factors contributing to the
rise and decline of beetle populations are poorly understood and epi-
demics are, therefore, unpredictable. Attempts to control the southern
pine beetle have usually been ineffective.

Thatcher (1960), Dixon and Osgood (1961) and Coulson et al
(1972) have reviewed southern pine beetle biology. The beetle produces
anywhere from two to eight generations per year depending on such fac-
tors as site, elevation, latitude and host type. After initial attach
and colonization parent adults are capable of re-emergence and sub-
sequent attack on other trees. Attacks often continue throughout the
year.

Brood adults emerge from infested trees to disperse by flight
and infest new host material. The developmental stages of the beetle
are passed within the host tissues. The developmental time averages
40 days (Franklin, 1969). The completion of brood emergence may take
20 or more days.

Females initiate gallery construction by formation of a nuptial
chamber. When joined by a male, a serpentine gallery is constructed
in the phloem layer of the bark. Trees are killed by the mechanical
girdling action of the adult and larval galleries and by the wilt
caused by blue-staining fungi of the genus Ceratocystis which are
introduced by attacking beetles (Barras, 1970).

The attack behavior of the southern pine beetle has been des-
cribed in studies by Gara (1967), Vite' and Crozier (1968), Gara and
Coster (1968) and Coster and Gara (1968). Suitable hosts are located
in dispersal flights by female beetles. Available evidence suggests

that the initial selection of host trees is random (Gara, Vité and Cramer, 1965). After the initial colonization by these pioneering females, adult D. frontalis mass attack the tree in response to a combination of insect- and host-produced attractants (Gara, Vité and Cramer, 1965; Renwick and Vité, 1970).

Renwick and Vité (1969) have suggested a mechanism for their action. Females initiating an attack on a tree release frontalin and trans-verbenol and stimulate resin exudation and release of alpha-pinene. This combination attracts large numbers of beetles. Successfully feeding beetles cease production of the pheromone principles. Aggregation of beetles on the tree then ceases. Mass aggregations of the beetle have been found to shift rapidly from one tree to another as attractive sources develop and decline, overwhelming one tree at a time in active infestations (Gara and Coster, 1968).

The infestation period is short. According to Franklin (1970), the pattern in an artificially induced attack sees an initial response by a few beetles the first day with an increase in activity the second day. The third or fourth day finds a mass attack by thousands of beetles after which the attack drops off as rapidly as it began.

Recent research on bark beetles has centered on control of these pests and many studies have focused on biological control agents. The roles of predators and parasites have received considerable attention, but few studies have documented their real impact on prey populations. Substantive data from which opinions might be formed have not been available.

The genera Enoclerus and Thanasimus of the family Cleridae con-

tain important predators of the Scolytidae (Chamberlin, 1939). Early investigators of these predators documented their associations with various bark beetle species (Hopkins, 1902; Keen, 1928; and Deleon, 1934). Person (1940) first commented on the possible significance of predation by a clerid on a bark beetle population, and Struble (1942) developed laboratory rearing methods for Enoclerus sphegeus (Fabricius) as a preliminary step to augment field populations of that predator.

Unfortunately, most investigations of the action and use of clerids in the control of bark beetles were discontinued with the advent of broad-spectrum chemical insecticides in the late 1940's. Since chemical controls of bark beetles have proved only moderately successful at best, the recent imposition of restrictions on the use of pesticides has stimulated renewed interest in biological control.

The role of clerids as bark beetle predators has recently received considerable attention and the biologies of a number of species have been worked out in some detail (Reid, 1957; Cowan and Nagel, 1965; Berryman, 1966a and 1966b; Schmid, 1970; and Rice 1969a). Amman (1970 and 1972) has studied prey consumption by the immature stages of Enoclerus sphegeus and Thanasimus undatulus Say. Rice (1969b) and Harwood and Rudinsky (1966) have discussed the role of olfactory attractants in clerid biology. The relative effectiveness of clerids as predators has been discussed at some length by Berryman (1970).

Thanasimus dubius is a predator of both the adult and larval stages of the southern pine beetle. The life cycles of the prey and predator are closely synchronized at the beginning of attack on a host tree, for mass aggregations of scolytids and clerids occur simultaneous-

ly (Vité and Crozier, 1968).

Vité and Williamson (1970) investigated the olfactory responses of T. dubius and found that the predator responds to the release of pheromones by the southern pine beetle (Figure 1). Clerid response was tested to the pheromones frontalin, trans-verbenol, verbenone and fractions of host tree oleoresins. Male and female T. dubius were found to respond equally in large numbers to frontalin. A lower level of response was found for trans-verbenol, whereas verbenone induced the least response of the insect produced volatiles and that predominately from the male clerids. Host tree oleoresin fractions were found to be much less attractive than the insect-produced volatiles. Combinations of the other volatiles with frontalin elicited no more response than that to frontalin alone.

Hatching of the clerid egg coincides with early instar activity of larval southern pine beetles permitting T. dubius larvae to feed on the immature stages of the prey. Larvae appear to move freely in the southern pine beetle galleries and may emerge to wander considerable distances about the bark surface before re-entering a gallery system (Dix, 1974).

The synchrony of the predator and prey life cycles becomes disrupted when the immature southern pine beetles complete their development in 35 to 40 days and emerge, for clerid development is slower. Larval clerids have been found to complete development in 67 to 83 days (Mignot and Anderson, 1969).

The diurnal and spatial activity patterns of T. dubius closely parallel those of the southern pine beetle (Thatcher and Pickard,

HOST TREE	IN-FLIGHT BEETLE POPULATIONS	PROPOSED ATTACK SEQUENCE
♀ ♀	♂♂♀♀ ♂♀	1. Initial attack by female southern pine beetles.
? ♀ frontalin trans-verbenol alpha-pinene	♂♂♀♀ ♂♀	2. Volatiles released.
? ♂ ♂ ? ♂ ♀ ♀ ♀	♂♂♀♀ ♂♀	3. Mass attack in response to insect-produced phero-mones and host produced terpenes + clerid response.
♂♀ ♂ ♂♀ ♀ ♂♀	♂♂♀♀ ♂♀	4. Cessation of pheromone production and oleoresin exudation.
♂♀ ♂♀ ♂♀	♂♂♀♀ ♂♀	5. Shift of attack by the southern pine beetle + clerid departure.

♂ – male Dendroctonus frontalis
♀ – female D. frontalis
♂ – male Thanasimus dubius
♀ – female T. dubius

Figure 1. Sequence of southern pine beetle attack and clerid response (adapted from Renwick and Vité, 1969).

1966). Peak adult activity of the clerid occurs during and just after host emergence from brood trees and their flight to attack other trees. Dix (1974), however, has observed nocturnal activity in the adult clerid and found that mating and searching activities continued after dark, but she reported no instances of nocturnal feeding.

Upon locating a tree undergoing southern pine beetle attack, T. dubius adults immediately begin searching and mating activities. Their movements on the bark surface are apparently random. The antennae are vibrated as the clerid moves but become motionless when it stops. Their specific function is unclear but they doubtless play some role in prey location. Matings are spontaneous, frequent and repeated.

Thanasimus dubius is opportunistic in its attack behavior. Adult prey insects are detected visually at distances ranging from 0 to 3 centimeters. Those prey individuals attacked at distances greater than 0.5 cm. are always moving. Stationary prey are seldom attacked but the slightest movement by the bark beetle induces immediate attack by the receptive clerid.

Prey handling techniques are similar to those described for Enoclerus lecontei (Wolcott) (Berryman, 1966b) and E. sphegeus (Schmid, 1971)[1]. The prey is grasped behind the prothorax and turned to expose the venter. While supporting itself on its metathoracic legs and abdomen, the clerid cradles the prey in its mesothoracic legs and manipulates it with its prothoracic legs. The clerid begins by eating through the soft intersegmental membranes separating the head and

[1]Personal communication, J. M. Schmid, 27 July 1971.

prothorax. The soft internal structures are consumed and the legs, elytra, wings and body exoskeleton are generally discarded.

Adult clerids remain on the tree to attack the adult southern pine beetles as long as they continue to arrive on the tree, and follow the bark beetles to new host trees in response to shifting centers of attraction (Anonymous, 1972).

The possible role of T. dubius in the control of the southern pine beetle has been commented on by Thatcher and Pickard (1966), but to date, little definitive work has been devoted to this subject. The present investigations were begun, therefore, to determine the significance of adult T. dubius predation on southern pine beetle populations. Studies were initiated to determine the effects of prey consumption on survivorship and oviposition. In addition, predator sex, age, size and ovipositional status were examined to determine possible effects on prey consumption rates.

MATERIALS AND METHODS

Rearing Techniques

Adults of T. dubius and D. frontalis were obtained by caging naturally infested sections of shortleaf pine (Pinus echinata Miller) and loblolly pine (Pinus taeda Linnaeus) in the laboratory. Beetles were collected from the screens as they emerged and used as needed. All clerids used in these investigations were collected within 24 hours of emergence.

Individual clerids were maintained in plastic petri dishes measuring 8.5 cm. inside diameter and 1.2 cm. in depth. Each dish

contained a single sheet of 1 qualitative 9 cm. Whatman filter paper.[2]
Approximately 0.6 ml. of distilled water was added to each dish daily
to maintain moisture in the filter paper. Humidity in the dishes was
at or near saturation. Filter paper and dishes were changed weekly.

Oviposition chambers used in these investigations were modeled
after Berryman (1966b). The design consisted of one pint plastic ice
cream containers to which had been added screened ventilation ports
(Figure 2). A 9 cm. sheet of filter paper covered the bottom. Clerid
females maintained in these containers were provided with a spirally
wrapped strip of paper toweling for an oviposition site (Struble,
1942).

All studies were conducted within a temperature range of 21 to
26 °C and under conditions of continuous light.

Sex Determination of Thanasimus dubius

Adult clerids were sexed by observing the sixth abdominal ster-
nite with a dissecting microscope as described for Enoclerus sphegeus
by Cowan and Nagel (1965). The sixth abdominal sternite in the female
of T. dubius is convex and generally extends to the apex of the abdo-
men (Figure 3). In the male the sixth abdominal sternite is emarginate
and rarely extends to the abdominal margin (Figure 4). The male
copulatory organ may or may not be partially exposed. Since only 68
of 203 males examined exhibited this latter characteristic, it could
not be used as a reliable sexing character. With experience, examina-

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[2]W and R Balston Limited.
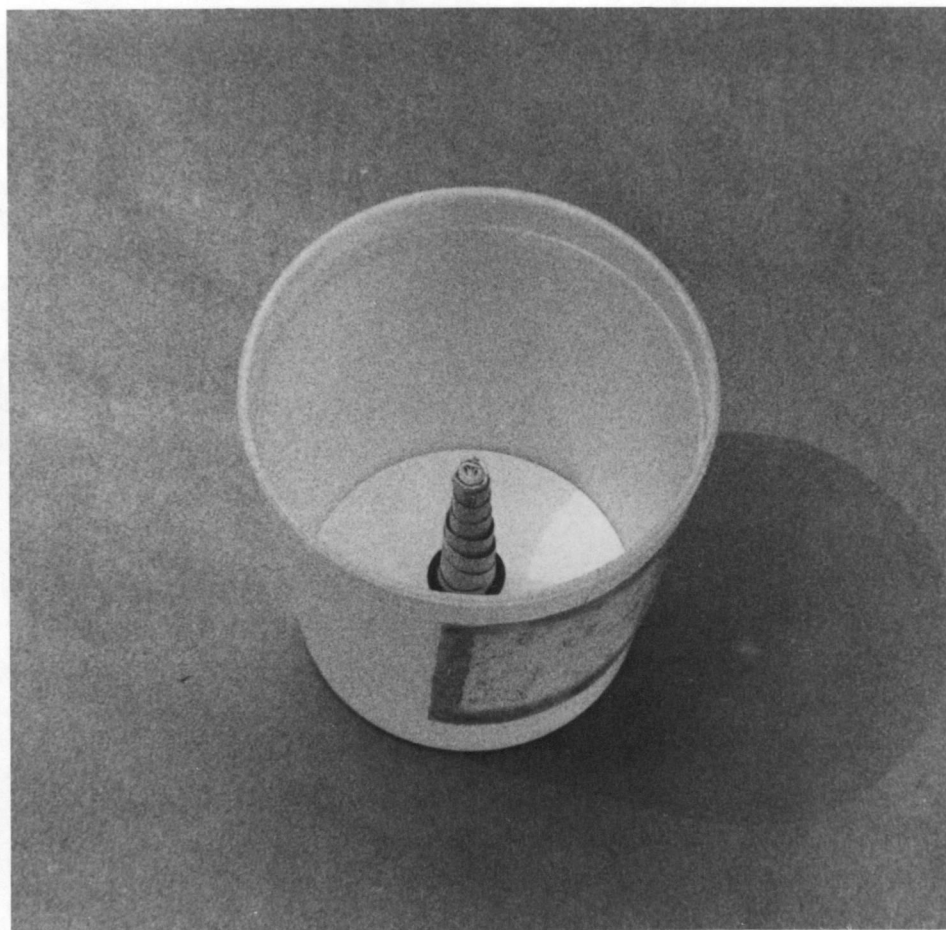
Figure 2. Chamber used for studying oviposition by _Thanasimus_ _dubius_ Fabricius.
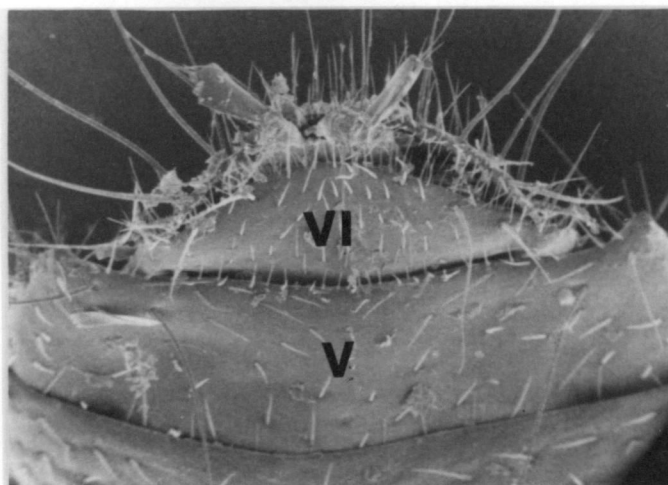
Figure 3. Scanning electron micrograph
           (100X) of the ventral surface of
           the abdomen of the female of
           Thanasimus _dubius_ Fabricius show-
           ing the secondary sexual charac-
           ter. Note that the sixth abdomi-
           nal sternite lacks emargination.
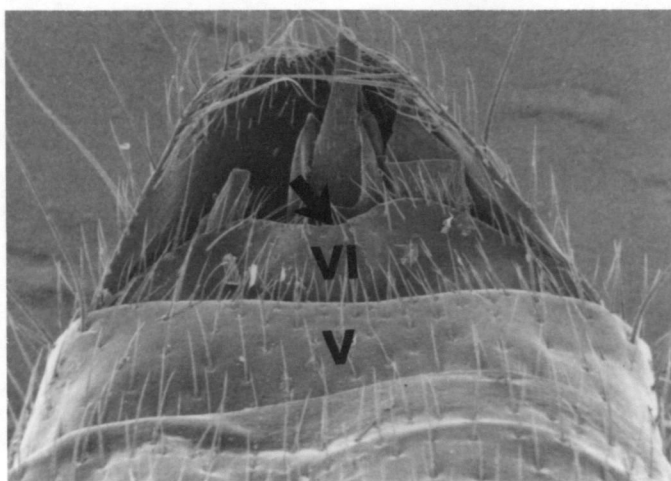
Figure 4. Scanning electron micrograph
           (100X) of the ventral surface of
           the abdomen of the male of
           Thanasimus _dubius_ Fabricius show-
           ing the secondary sexual charac-
           ter. Note that the sixth abdomi-
           nal sternite is emarginate (arrow).

tion of the sixth abdominal sternite proved to be 100 percent accurate.
Over 400 determinations were subsequently confirmed by dissection.

Predator Size

Body length and total weight were measured after the death of
individuals. The flexibility and elasticity of membranes separating the
head from the prothorax and the prothorax from the abdomen produced
considerable variation in interpretation of body length. Body length,
therefore, was discarded as an index of predator size. Weights of
preserved specimen material also proved unsatisfactory.

Elytral length, therefore, was used as an index of predator
size. Measurements were taken along the sutural line separating the
elytra and determined to the nearest 0.1 mm. by means of a dissecting
microscope equipped with an ocular micrometer.

Activity Patterns of Predator and Prey

In mid-March, 1972 attempts were begun to induce attack on a
pine tree in order to investigate the attack pattern of the southern
pine beetle and arrival sequence of clerid predators and secondary bark
beetle species. The tree selected was a dominant shortleaf pine (Pinus
echinata Miller) some 36 m. in height and 30 cm. d.b.h. The southern
pine beetles were attracted by using fresh pine bolts into which females
had been introduced as described by Franklin (1970). The bolts
measured 50 cm. in length and 10 to 15 cm. in diameter, and were in-
fested by approximately 100 females over a 12 to 18 hour period prior
to use. The bolts were suspended from the tree at 4.5 meters and were

replaced at two to three day intervals until attack had begun.

Aluminum wire screens (18 x 16 mesh)[3] measuring 15.25 cm. on a side and coated with Stikem Special[4] were placed at 0, 1.5, 2.2, 3.0, 4.5, 6.0, 7.5 and 9.0 meters on the bole surface. All screens were placed on the southeast aspect of the bole. Screens were inspected at one to two day intervals and all bark beetles and clerids removed and counted.

Prey Specificity

Clerids predatory on bark beetle species have rarely been reported as predators of species of other taxons. Struble (1942) in repeated tests with Enoclerus sphegeus was unable to make use of prey other than bark beetles.

Thanasimus dubius has been implicated only as a predator of bark beetle species of the family Scolytidae. To test the limits and range of prey acceptance a wide range of Scolytidae and a selection of insect species associated with the southern pine beetle were offered as prospective prey. In addition, three common laboratory grain beetles, Sitophilus oryzae (Linnaeus), Oryzaephilus surinamensis (Linnaeus) and a Tribolium sp. were tested. Specimens for these investigations were obtained from laboratory culture, light trap collection or by rearing them from infested wood. Test animals were offered to clerids for a period of 48 hours and considered rejected if not

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[3]Phirer Wire Products.

[4]Michel and Pelton Co.

consumed during that period.

Feeding Time and Prey Utilization

Feeding by 80 T. dubius adults was observed and handling times recorded. To determine if predator feeding history or sex affected feeding time, prey were presented to groups of 20 clerids at rates of 1.00, 0.50, 0.33 and 0.25 prey per day. Each group of 20 clerids contained 10 male and 10 female individuals. Feeding activity was timed from initial attack until post-feeding grooming had begun. The student's t-test was used to determine if differences in handling time could be discerned.

To investigate prey utilization by the two sexes, 100 southern pine beetle adults were fed to 10 male and 10 female T. dubius adults over a five-day-period. Each clerid consumed one prey daily. Each prey was weighed prior to consumption and those parts of the scolytid not consumed were collected and weighed. Weights were determined to the nearest tenth of a milligram. Prey beetles were assigned to clerids at random.

Prey Consumption

The effects of prey consumption rate on adult T. dubius longevity and oviposition were investigated. In addition, predator sex, size, age and female ovipositional status were examined for possible effects on prey consumption.

To investigate the effects of prey consumption rate on longevity,

424 adult clerids were maintained on nine feeding schedules with prey availabilities ranging from 0 to 4 prey per day (TABLE I). All clerids were collected and maintained individually as described above. Unsexed and unsized prey beetles were assigned to predators at random. Records were maintained of predator longevity, number of prey offered and number of prey consumed for the adult life of each clerid.

Thanasimus dubius oviposition was studied at two prey consumption rates. Upon emergence females were isolated in individual oviposition chambers and feeding regimens were established. Ten female clerids received prey at the rate of 4.0 per day and another 10 female clerids received prey at the rate of 0.5 per day. Access to males was provided for two hours daily for purposes of mating.

As Mignot and Anderson (1969) had determined that a preovipositional period of up to seven days was required, records of oviposition and prey consumption were established on day seven after isolation and continued for thirty days.

Field Density of Thanasimus dubius

Two field estimates of predator density were obtained from four shortleaf pines undergoing southern pine beetle mass attack. The first method consisted of making a count of clerids on a unit area of bole surface and extrapolating the tree population from the sample estimate. The surface area of a tree was estimated from height and diameter measurements. Twenty counts were taken from the four trees on days one through five of the attack sequence.

The second method consisted of placing eight 15.25 cm. square

TABLE I.   FEEDING SCHEDULES USED IN THE STUDY OF PREY CONSUMPTION BY
           ADULT THANASIMUS DUBIUS FABRICIUS

Feeding Schedule	Feeding Rate (prey per day)	Feeding Program	Number of Clerids on Schedule
I	4.000	4 southern pine beetles per day	24
II	1.000	1 southern pine beetle per day	50
III	0.500	1 southern pine beetle every 2nd day	50
IV	0.333	1 southern pine beetle every 3rd day	50
V	0.250	1 southern pine beetle every 4th day	50
VI	0.200	1 southern pine beetle every 5th day	50
VII	0.167	1 southern pine beetle every 6th day	50
VIII	0.143	1 southern pine beetle every 7th day	51
IX	0	no feeding	49

aluminum screen traps coated with Stikem Special at 1.5 meter intervals up the bole surface. Clerids were removed and counted at 24 hour intervals. Clerids trapped were considered as new arrivals to the tree during any 24 hour period as it was found that contact with the traps generally occurred on landing from flight. A tree population for the clerid was extrapolated based on estimates of tree surface area. Twenty counts were taken from the four trees on days one through five of the attack sequence.

RESULTS

Predator Size

Frequency distributions for the size of adult male and female T. dubius are presented in Figures 5 and 6. Male elytral lengths averaged 4.53 ± 0.06 mm. for 200 observations. Female elytral lengths averaged 4.72 ± 0.06 mm. for 200 observations. The use of the student's t-test to compare the two means indicated that T. dubius females were significantly larger than males ($t_{95} < 1.6449$, 422 d.f.). However, elytral lengths of males ranged from 3.6 to 5.6 mm. and those of females ranged from 3.6 to 5.9 mm. Thus, while sex is a determinant of relative size, it seems probable that larval feeding history is the most significant factor in determining the size of any individual clerid.

Activity Patterns of Predator and Prey

Arrival sequences for the southern pine beetle, three species of
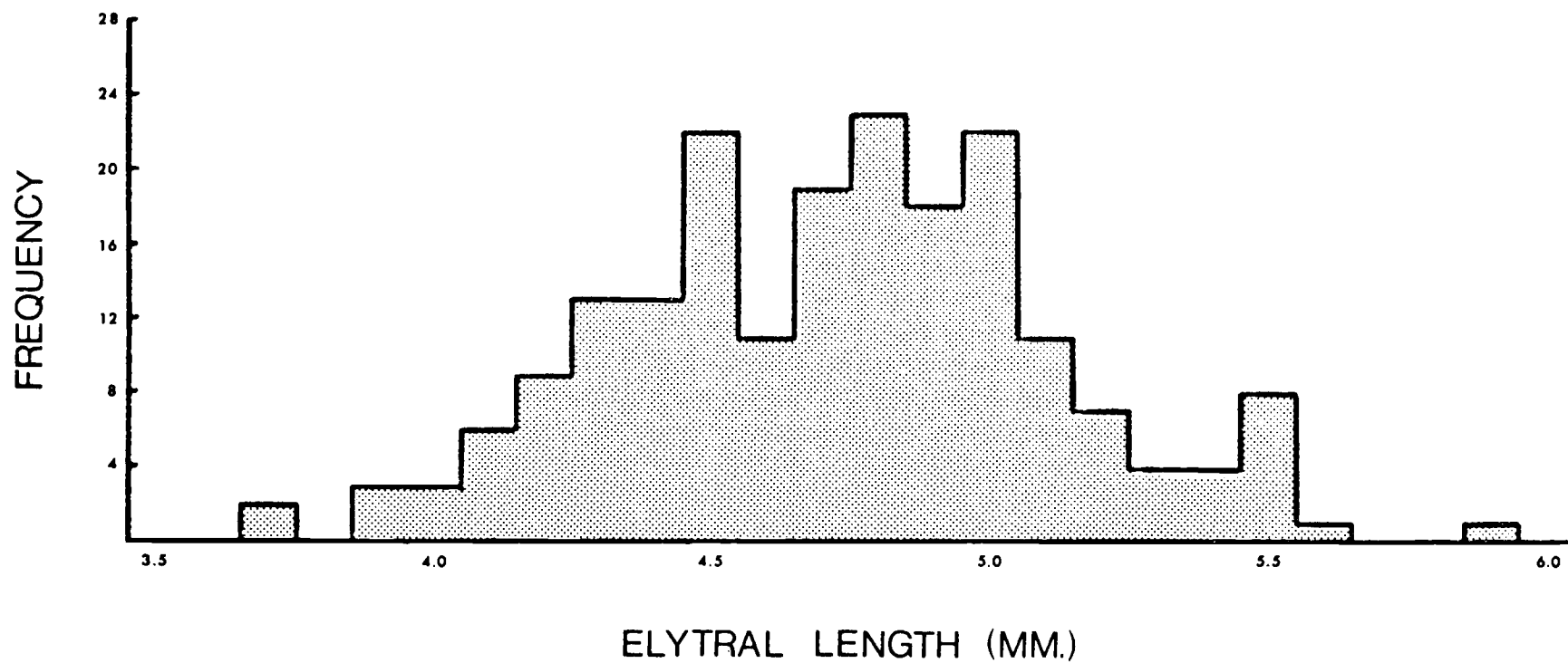
Figure 5. Frequency distribution for elytral lengths of 200 adult female Thanasimus dubius Fabricius.
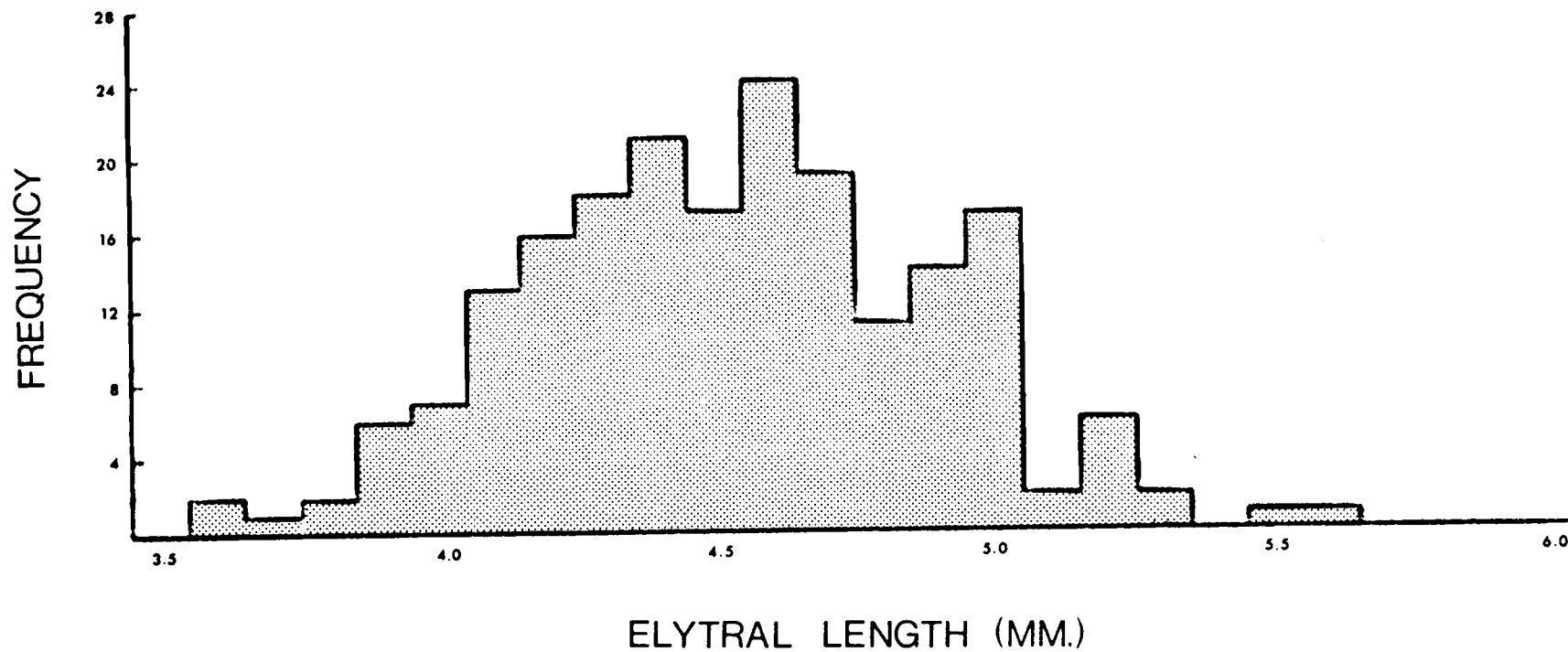
Figure 6. Frequency distribution for elytral lengths of 200 adult male *Thanasimus dubius* Fabricius.

Ips beetles and two clerid species are presented in Figure 7. Only
occasional response by the southern pine beetle to the attractive
source was observed until April 7-8 at which time a slight increase in
activity was noted. The first pitch tubes indicating attack were found
on April 10. A mass attack occurred on April 11-12 during which a
total of 1763 southern pine beetle adults were trapped. The activity
dropped off rapidly in succeeding days.

Ips spp. attacks, which began on April 17-18 and continued for
six days, were confined largely to the bole above 6 meters.

Only ten T. dubius and three Enoclerus nigripes (Say) were
trapped, but their distribution on the bole and time of arrival seem
significant. Thanasimus dubius was first trapped on April 5-6, before
the mass attack had occurred and individuals were caught for as long as
the southern pine beetle attack continued. Distribution on the bole
appeared to follow closely the shifts of southern pine beetle activity.
Enoclerus nigripes, on the other hand, did not appear until after the
Ips attacks were well under way and southern pine beetle activity on
the bole surface had ceased.

Prey Specificity

The range of prey suitability for adult T. dubius is apparently
restricted to the family scolytidae. Members of that family showing
wide variation in size, form and host preference were consumed. Six-
teen species of Scolytidae representing three subfamilies and nine
tribes were accepted as prey (TABLE II). Species representing other
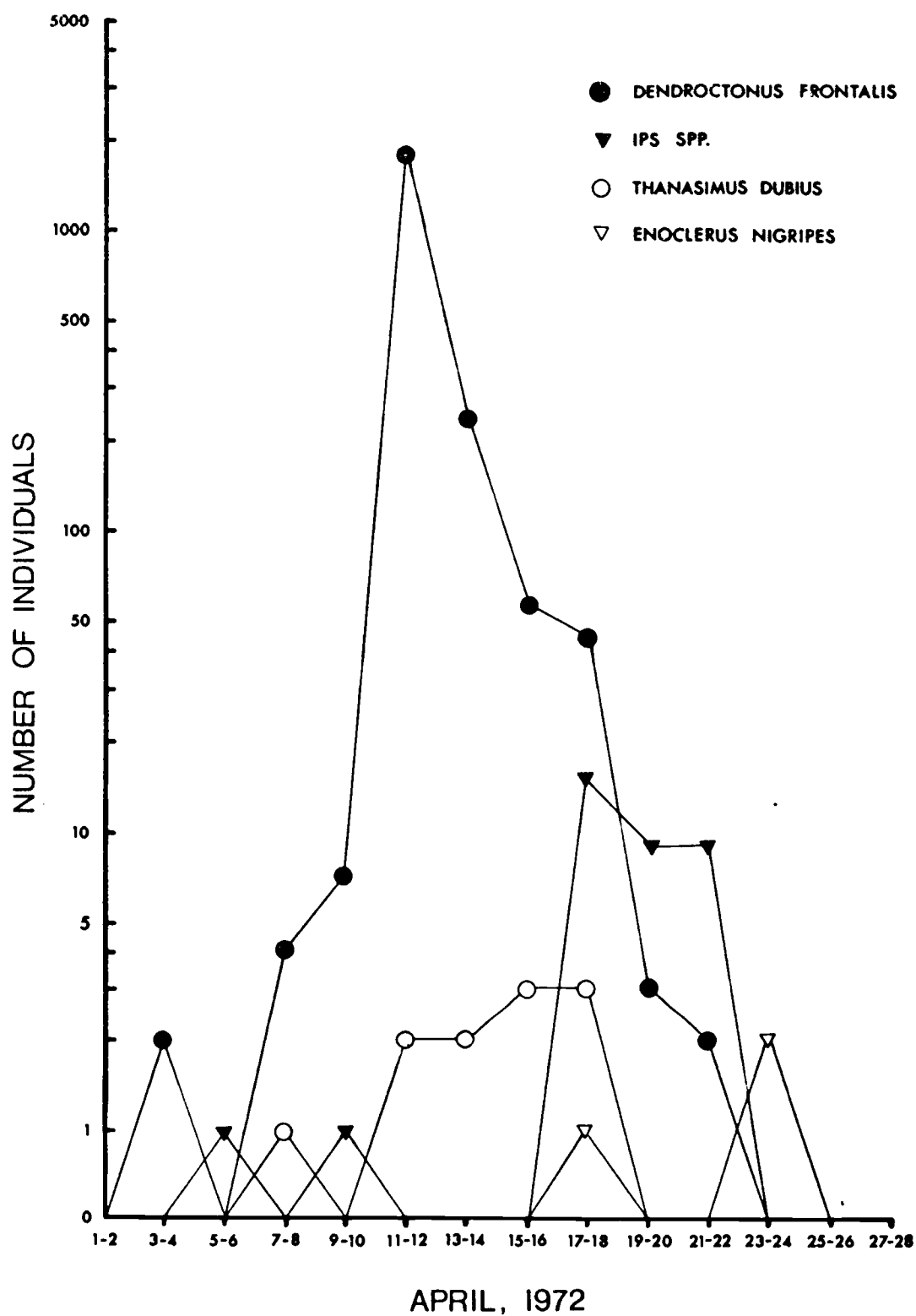
Figure 7. Arrival sequence of bark beetle (Scolytidae) and clerid (Cleridae) species on a shortleaf pine undergoing southern pine beetle attack in April, 1972.

TABLE II.   INSECT SPECIES ACCEPTED AS PREY BY ADULT THANASIMUS DUBIUS FABRICIUS

Species[5]

Dendroctonus frontalis Zimmerman

Dendroctonus terrebrans (Olivier)

Gnathotrichus materiarius Fitch

Hylastes sp. (porculus Erichson or salebrosus (Eichhoff))

Hylastes tenuis Eichhoff

Ips avulsus (Eichhoff)

Ips calligraphus (Germar)

Ips grandicollis (Eichhoff)

Ips pini Say

Orthotomicus caelatus (Eichhoff)

Phloeosinus dentatus (Say)

Pityophthorus bellus Blackman

Polygraphus rufipennis Kirby

Pseudopityophthorus pruinosus (Eichhoff)

Scolytus multistriatus (Marsham)

Xyleborus sp. (prob. pubescens Zimmerman)

[5]All order Coleoptera, family Scolytidae.

taxons were rejected (TABLE III). Observations of clerid activity under test conditions indicated that visual or physical contact with these prospective prey elicited no more than cursory examinations.

Most, it not all predators, are responsive to a specific size of prey and less readily attack prey smaller or larger than this optimum (Holling, 1964). Otherwise acceptable prey may be rejected on the basis of size alone. Crypturgus alutaceus Schwarz was the sole scolytid species rejected and it must be noted that it is a very small species.

Feeding history can also affect prey recognition. Thanasimus dubius feeding for extended periods of time on the southern pine beetle less readily attacked scolytids very much larger or smaller than that standard. Prey species of comparable size, for example Ips grandicollis, were readily accepted after such conditioning.

Feeding Time and Prey Utilization

Feeding times for 80 observations varied from 3.05 to 22.19 minutes with a mean of 11.38 $\pm$ 0.46 minutes. Handling time did not vary significantly with predator sex ($t_{95} < 1.6647$, 78 d.f.), and no differences could be discerned in feeding times at the various prey availability levels ($t_{95} < 1.6766$, 38 d.f.) (TABLE IV).

Ingestion (as measured by weight) was determined by prey size. The proportion of an attacked individual that was consumed remained relatively constant (mean = 79.4 percent). Utilization rates for the two sexes (TABLES XXII and XXIII of the appendices) showed no signi-

TABLE III. INSECT SPECIES REJECTED AS PREY BY ADULT THANASIMUS DUBIUS
            FABRICIUS

Order, Family and Species

COLEOPTERA
        Colydiidae
                Aulonium sp.
                Colydium nigripennis Leconte
        Cucujidae
                Oryzaephilus surinamensis (Linnaeus)
        Curculionidae
                Pissodes sp.
                Sitophilus oryzae (Linnaeus)
        Histeridae
                Cylistix cylindricus Paykull
        Ostomidae
                Corticotomus sp.
                Tenebroides sp.
        Platypodidae
                Platypus compositus Say
                Platypus flavicornis (Fabricius)
        Scolytidae
                Crypturgus alutaceus Schwarz
        Tenebrionidae
                Corticeus nr. parallelus (Melsheimer)
                Tribolium sp.
DIPTERA
        Dolichopodidae
                Medetera sp.
        Lonchaeidae
                Lonchaea sp.
HYMENOPTERA
        Braconidae
                Coeloides sp.
        Eurytomidae
                Eurytoma sp.
        Pteromalidae
                Heydenia unica Cook & Davis
        Torymidae
                Roptrocerus sp.

TABLE IV. FEEDING TIMES FOR ADULT THANASIMUS DUBIUS FABRICIUS WITH
ADULT SOUTHERN PINE BEETLES AS PREY

Predator Sex	Availability of Prey (per day)	Mean Feeding Time (minutes)	Standard Error	Number of Observations
male	--	12.88	0.54	16
female	--	11.92	0.37	31
--	1.00	10.99	0.47	20
--	0.50	13.51	0.42	20
--	0.33	13.87	0.45	20
--	0.25	10.86	0.46	20

ficant difference ($t_{95} < 1.6606$, 98 d.f.).

Prey Consumption

Mean daily prey consumption rates for T. dubius adults on the
nine feeding schedules followed in the present studies are presented
in TABLE V. Prey consumption increased directly with prey availabil-
ity to the level of 1.28 prey per day. Prey offered in excess of this
number were not consumed.

Mean longevities for the nine feeding schedules are presented in
TABLE VI. Survivorship curves are shown in Figures 8 through 16.
Mean longevities ranged from 16.94 days for feeding schedule IX to
95.98 days for feeding schedule II. Individual longevities ranged from
9 to 262 days.

The effect of prey consumption on adult T. dubius longevity is
depicted graphically in Figure 17. Regression analysis indicated that
at most consumption rates longevity was effectively determined by the
number of prey consumed per day. Only when prey availability exceeded
the consumption rate was the correlation diminished (TABLE VII). Mean
longevities for females at all feeding rates were greater than for
males (Figure 18), but the differences were not significant.

Prey consumption had a marked effect on oviposition by female
clerids. Daily oviposition on feeding schedule I (TABLE VIII) had a
mean of 2.22 ± 0.20 for ten females. Maximum oviposition for any one
day was 10. Maximum oviposition for any thirty day period was 90.
Daily oviposition on feeding schedule III (TABLE IX) had a mean of
0.45 ± 0.03 for ten females. Maximum oviposition for any one day was 2.

TABLE V. DAILY CONSUMPTION OF ADULT SOUTHERN PINE BEETLES BY ADULT
THANASIMUS DUBIUS FABRICIUS FOR VARIOUS PREY AVAILABILITY
SCHEDULES[6]

Feeding Rate (prey/day)	Number of Clerids	Mean Daily Prey Consumption	Standard Error
4.00	24	1.28	0.25
1.00	50	0.91	0.13
0.50	50	0.49	0.10
0.33	50	0.33	0.00
0.25	50	0.25	0.01
0.20	50	0.20	0.00
0.17	50	0.17	0.01
0.14	51	0.14	0.01
0.00	49	0.00	--

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[6]Data summaries for individual clerids on the nine feeding
schedules are provided in the appendices (TABLES XIII through XXI).

TABLE VI. ADULT <u>THANASIMUS</u> <u>DUBIUS</u> FABRICIUS LONGEVITY IN THE LABORATORY
ON FEEDING SCHEDULES I THROUGH IX

Feeding Rate (prey/day)	Mean Longevity (days)	Standard Error	Mean Male Longevity (days)	Standard Error	Mean Female Longevity (days)	Standard Error
4.000	83.00	7.99	78.80	9.56	90.33	4.45
1.000	95.98	7.02	90.05	6.91	99.93	7.15
0.500	88.74	7.04	84.92	7.48	92.88	7.29
0.333	94.38	7.75	82.83	9.28	99.30	7.54
0.250	47.90	3.22	44.91	3.79	50.25	2.74
0.200	45.70	3.44	42.75	2.66	48.58	4.11
0.167	28.62	1.32	26.25	1.20	30.81	2.44
0.143	26.94	1.39	24.91	1.36	28.48	1.40
0.000	16.94	0.90	16.67	0.75	18.09	0.66
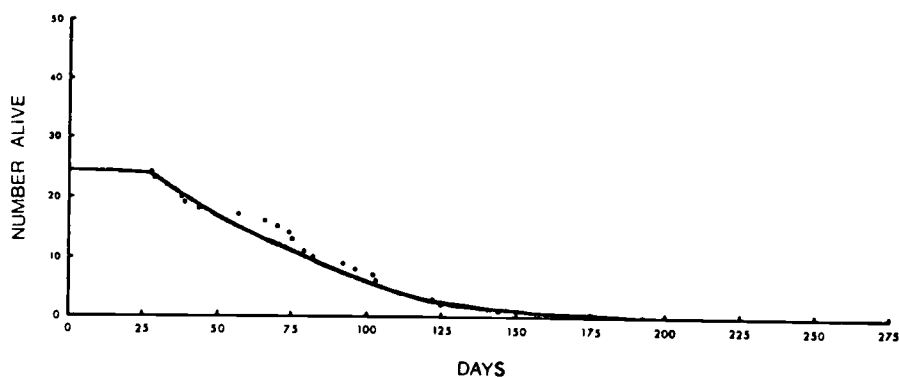
Figure 8. Survivorship curve for adult _Thanasimus dubius_ Fabricius receiving 4.0 prey per day.
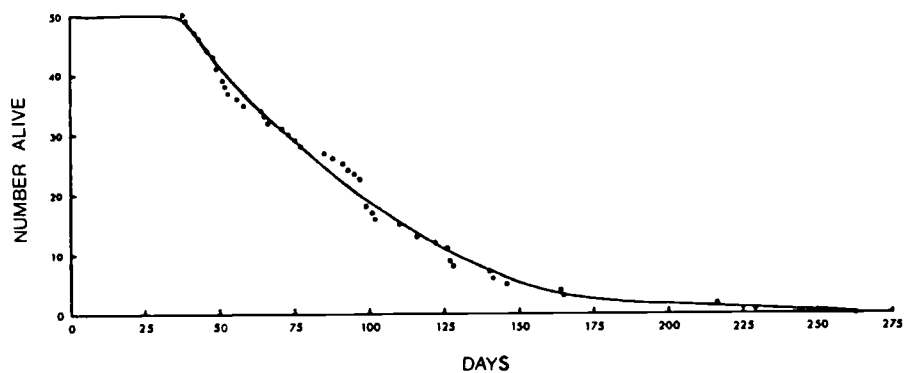
Figure 9. Survivorship curve for adult _Thanasimus dubius_ Fabricius receiving 1.0 prey per day.
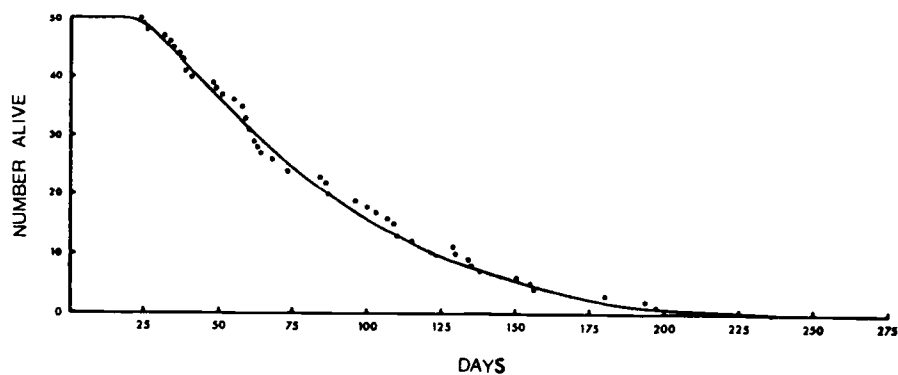
Figure 10. Survivorship curve for adult _Thanasimus dubius_ Fabricius receiving 0.5 prey per day.
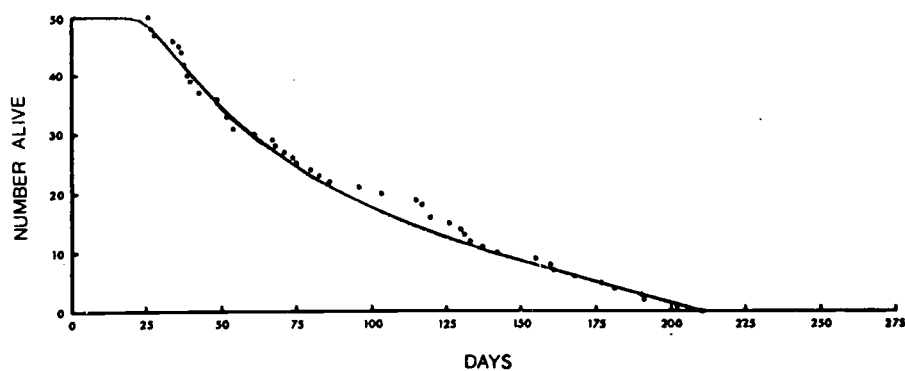
Figure 11. Survivorship curve for adult Thanasimus dubius
Fabricius receiving 0.33 prey per day.
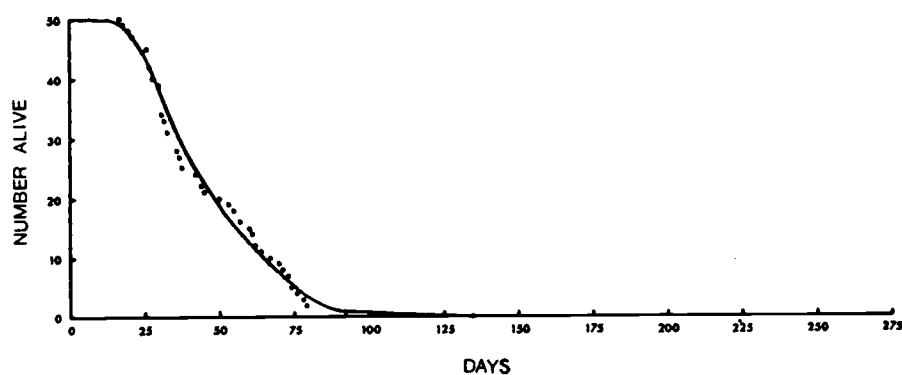
Figure 12. Survivorship curve for adult Thanasimus dubius
Fabricius receiving 0.25 prey per day.
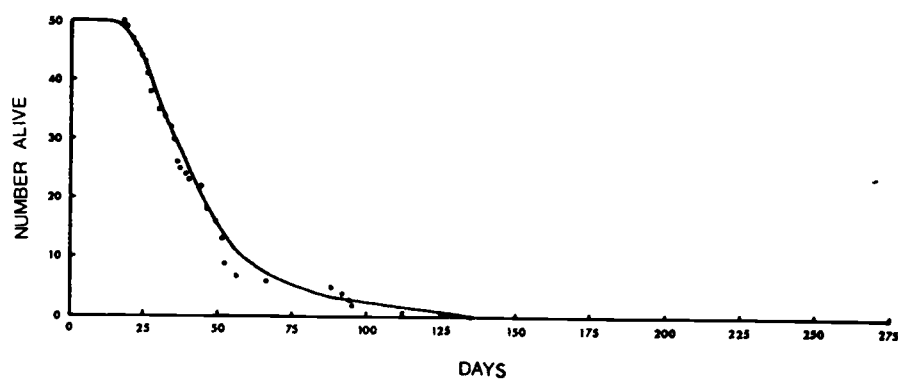
Figure 13. Survivorship curve for adult Thanasimus dubius
Fabricius receiving 0.20 prey per day.
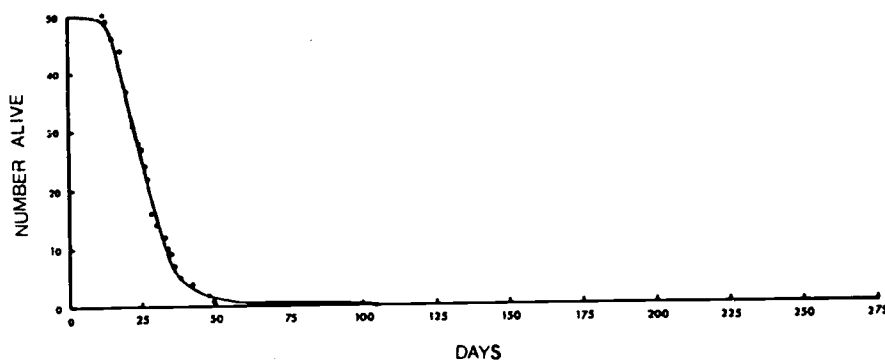
Figure 14. Survivorship curve for adult Thanasimus dubius Fabricius receiving 0.17 prey per day.
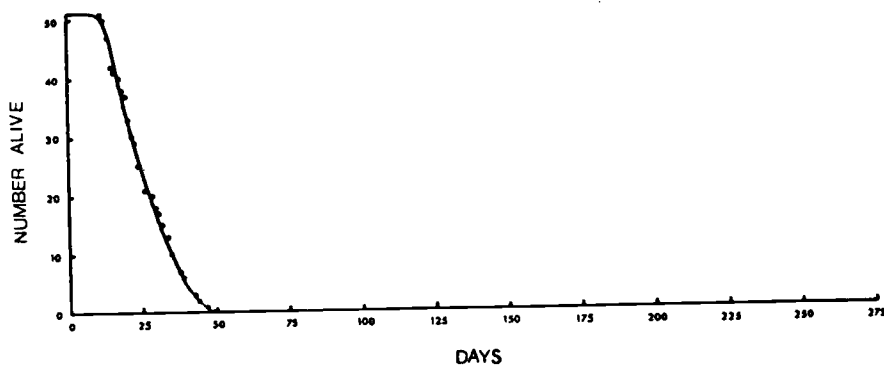
Figure 15. Survivorship curve for adult Thanasimus dubius Fabricius receiving 0.14 prey per day.
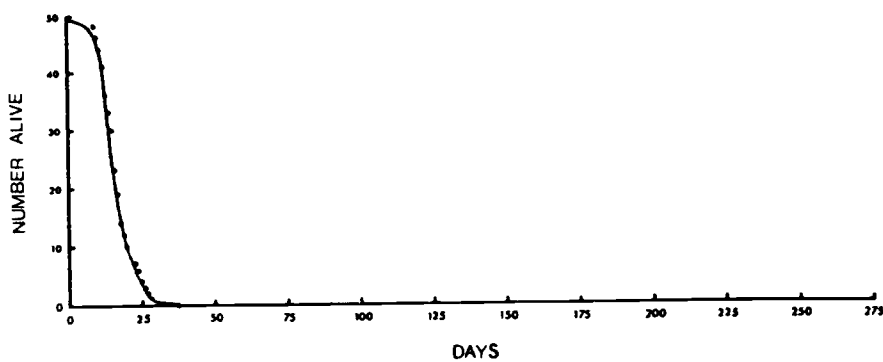
Figure 16. Survivorship curve for adult Thanasimus dubius Fabricius receiving 0.0 prey per day.
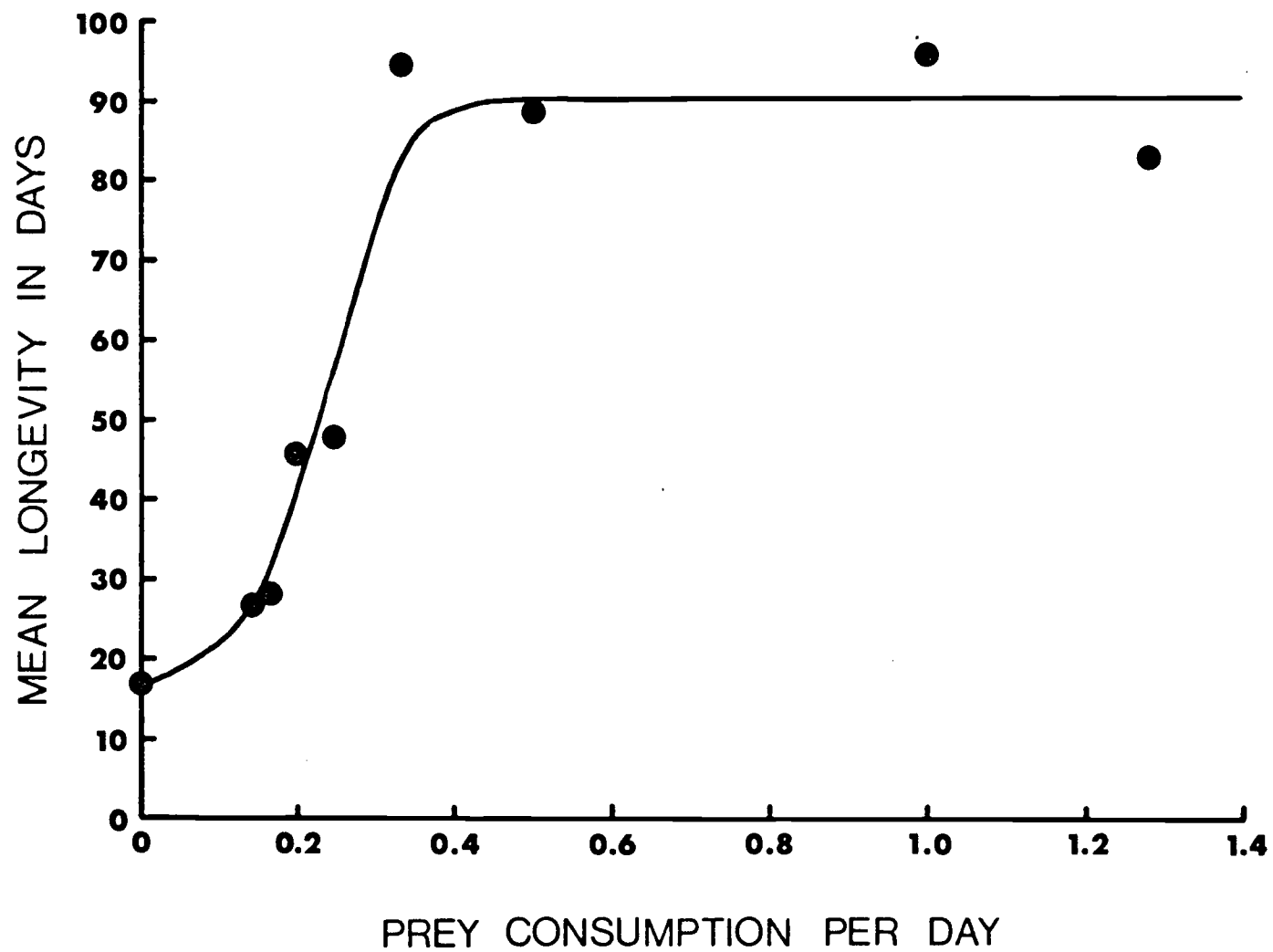
Figure 17. The effect of prey consumption on adult <u>Thanasimus</u> <u>dubius</u> Fabricius longevity.

TABLE VII. CORRELATION COEFFICIENTS AND SIGNIFICANCE VALUES FOR
REGRESSION ANALYSES ON CLERID LONGEVITY AGAINST PREY
CONSUMPTION

Feeding Schedule	r	r^2	t	n
I	0.683	0.467	4.39	24
II	0.989	0.978	41.37	50
III	0.998	0.996	116.47	50
IV	0.999	0.998	158.60	50
V	0.996	0.992	78.43	50
VI	0.994	0.998	62.14	50
VII	0.973	0.948	29.76	50
VIII	0.975	0.951	30.74	51
IX	--	--	--	49
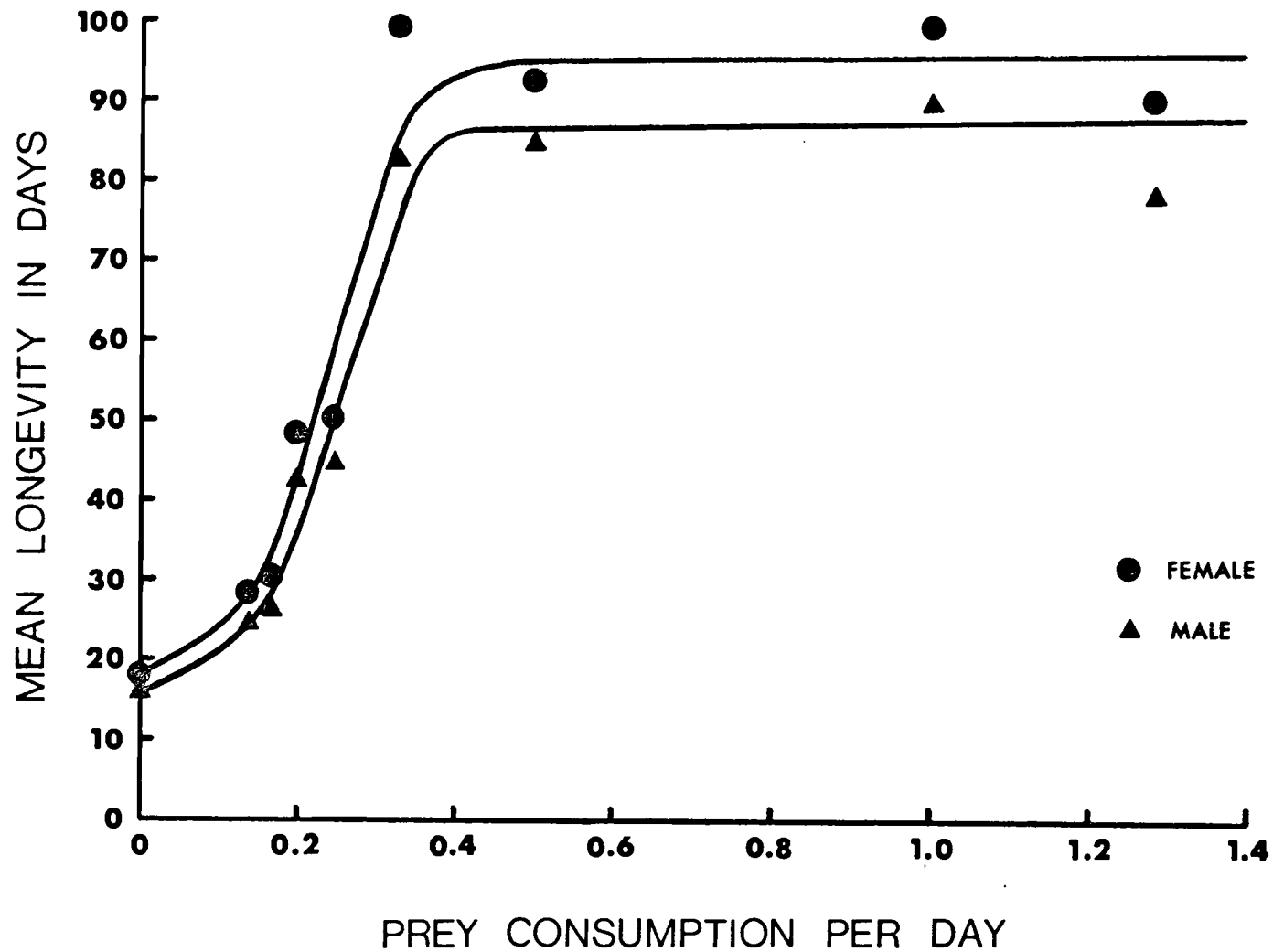
Figure 18. The effect of prey consumption on adult male and female Thanasimus dubius Fabricius longevity.

TABLE VIII. THIRTY DAY OVIPOSITION AND PREY CONSUMPTION RECORDS FOR
ADULT FEMALE <u>THANASIMUS</u> <u>DUBIUS</u> FABRICIUS RECEIVING 4.0
PREY PER DAY

Clerid Number	Total Oviposition	Oviposition Per Day	Total Prey Consumption	Prey Consumption Per Day	Oviposition Per Prey Consumed
1	59	1.96	74	2.47	0.80
2	62	2.07	70	2.33	0.89
3	90	3.00	91	3.03	0.99
4	50	1.67	62	2.07	0.81
5	66	2.20	79	2.63	0.84
6	60	2.00	67	2.23	0.90
7	74	2.47	80	2.67	0.93
8	59	1.96	58	1.93	1.02
9	82	2.73	75	2.50	1.09
10	64	2.13	87	2.90	0.74
Mean	66.6	2.22	74.3	2.48	0.90

TABLE IX.   THIRTY DAY OVIPOSITION AND PREY CONSUMPTION RECORDS FOR ADULT
FEMALE THANASIMUS DUBIUS FABRICIUS RECEIVING 0.5 PREY PER DAY

Clerid Number	Total Oviposition	Oviposition Per Day	Total Prey Consumption	Prey Consumption Per Day	Oviposition Per Prey Consumed
1	13	0.43	15	0.50	0.87
2	16	0.53	15	0.50	1.07
3	14	0.47	15	0.50	0.93
4	20	0.67	15	0.50	1.33
5	13	0.43	15	0.50	0.87
6	12	0.40	15	0.50	0.80
7	10	0.33	15	0.50	0.67
8	11	0.37	15	0.50	0.73
9	16	0.53	15	0.50	1.07
10	11	0.37	15	0.50	0.73
Mean	13.6	0.45	15	0.50	0.91

Maximum oviposition for any thirty day period was 20.

The prey consumption rate of adult clerids did not vary signi-
ficantly with time over the first 100 days of adult life (TABLE X
and Figure 19). The available data for age groups beyond 100 days,
unfortunately, were too limited to draw significant conclusions. While
there were obvious differences between predators, individual consump-
tion rates did not change with increasing age. Apparently age did not
hinder predator efficiency.

Larger clerids were found to consume more prey individuals.
Clerids larger than the mean (see section on predator size) were found
to consume an average of 1.40 prey per day when prey availability was
not limiting. Clerids smaller than the mean were found to consume an
average of 1.09 prey per day under the same conditions. The 95%
confidence interval of the difference between the two means was esti-
mated to be between 0.24 and 0.38 prey per day and hence, the differ-
ences were significant.

Female clerids were found to consume more prey than their male
counterparts. The data for daily prey consumption by male and non-
ovipositing females clerids when prey availability was not limiting
showed that the non-ovipositing females consumed a mean of 1.34 prey
per day while the males consumed 1.16 prey per day. The 95% confidence
interval for the difference between the two means was estimated as
between 0.11 and 0.25 prey per day, again indicating a significant
difference. It has been shown above, however, that female clerids are
generally larger than males, and any differences apparent between the
consumption rates of male and non-ovipositing female clerids are likely

TABLE X.   PREY CONSUMPTION BY ADULT THANASIMUS DUBIUS FABRICIUS
           WITH REFERENCE TO PREDATOR AGE

Age Interval x (days)	Number of Observations	Mean Number of Prey Consumed During x	Standard Error	Cumulative Mean Number of Prey Consumed
1 - 25	24	32.79	2.36	32.79
26 - 50	18	29.94	2.80	62.73
51 - 75	14	34.21	3.85	96.94
76 - 100	8	32.13	5.30	129.07
101 - 125	3	22.33	7.70	151.40
126 - 150	1	21.00	0.00	172.40
151 - 175	1	23.00	0.00	195.40
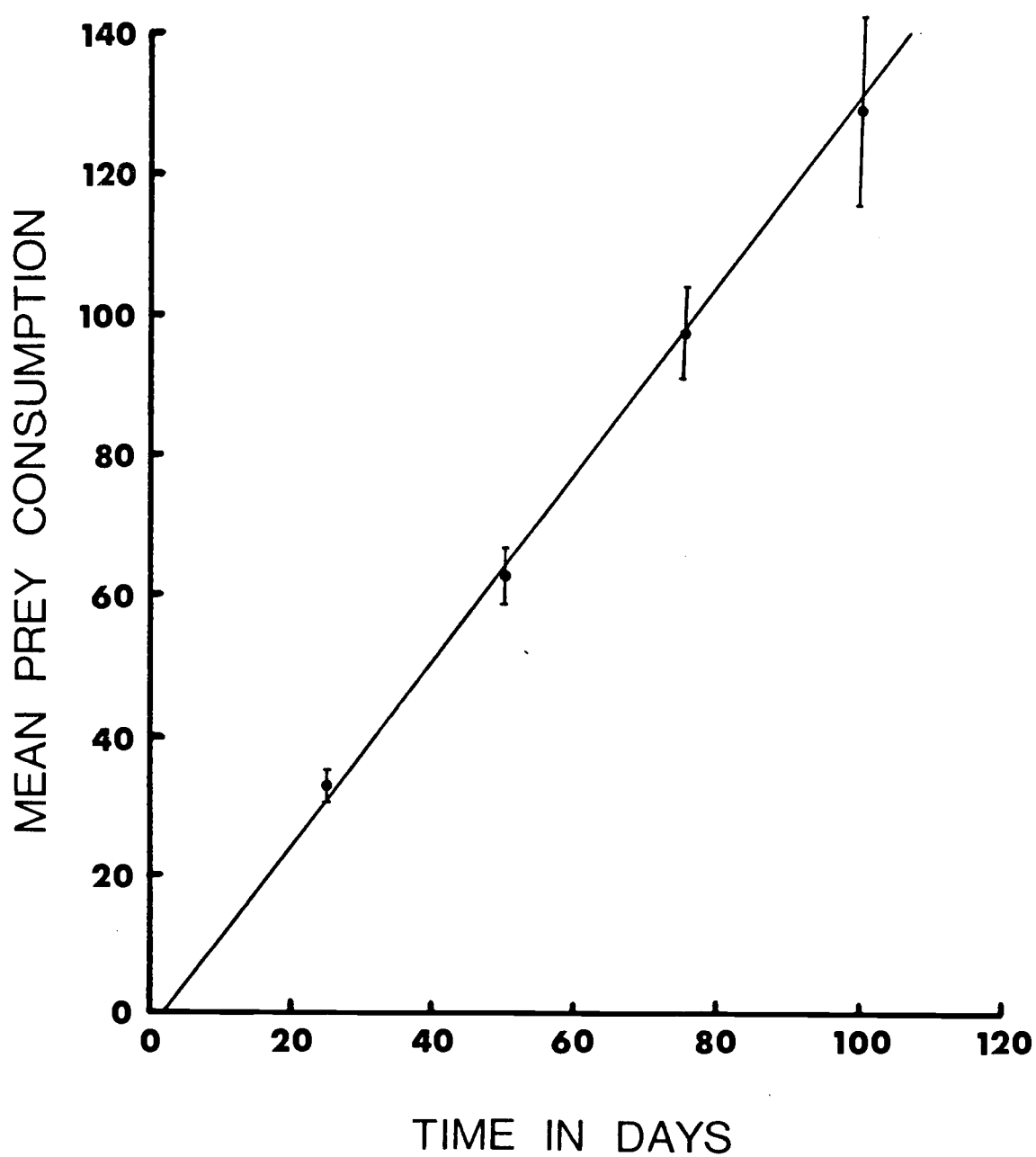
Figure 19. The effect of age on prey consumption by adult
Thanasimus dubius Fabricius.

attributable to difference in size.

The ovipositional status of the female had a pronounced effect on rate of prey consumption. Daily consumption rates for ovipositing females were nearly double those of non-ovipositing females (2.48 versus 1.34 prey per day).

Analysis of covariance was performed on the variables prey consumption, longevity, predator sex and predator size for the various feeding schedules. Significant relationships between both body size and sex and predator longevity were indicated, but these relationships did not contribute significantly to the overall correlation of longevity with prey consumption. Correlation coefficients for predator size and sex when food was not limiting, for example, were only 0.052 and 0.021, respectively.

Field Density of Thanasimus dubius

The counts from sticky screen traps are presented in TABLE XI. The maximum number of clerids counted on the screens from any 24 hour period was three (range 0-3). The average number trapped was 1.2 ± 0.3. Estimates of predator arrivals for 24 hour periods ranged from 0 to 83.2 per day. The average estimate was 29.8 clerids per day.

Predator density estimates by visual counts are presented in TABLE XII. The maximum number of clerids counted on one half of the bole surface of a tree to a height of six meters was 25 (range 0-25). The average number counted was 7.5 ± 1.5. Estimates of per tree clerid populations by this technique ranged from 0 to 116.7. The average

TABLE XI. FIELD ESTIMATES BY STICKY SCREEN COUNTS OF ADULT THANASIMUS
DUBIUS FABRICIUS DENSITY ON FOUR TREES DURING THE FIVE DAY
PERIOD FOLLOWING MASS ATTACK BY THE SOUTHERN PINE BEETLE

Tree Number	Day of Mass Attack	Number of Clerids Trapped	Tree Population Estimate
1	1	2	45.1
1	2	2	45.1
1	3	1	22.6
1	4	3	36.5
1	5	0	0.0
2	1	3	72.8
2	2	2	48.6
2	3	2	48.6
2	4	1	24.3
2	5	0	0.0
3	1	3	74.2
3	2	2	49.5
3	3	1	24.7
3	4	2	49.5
3	5	0	0.0
4	1	3	83.2
4	2	2	55.5
4	3	1	27.8
4	4	0	0.0
4	5	0	0.0

TABLE XII. FIELD ESTIMATES BY VISUAL COUNTS OF ADULT <u>THANASIMUS</u> <u>DUBIUS</u>
DENSITY ON FOUR TREES DURING THE FIVE DAY PERIOD FOLLOWING
MASS ATTACK BY THE SOUTHERN PINE BEETLE

Tree Number	Day of Mass Attack	Number of Clerids Observed	Tree Population Estimate
1	1	11	47.7
1	2	17	73.7
1	3	9	32.3
1	4	3	7.0
1	5	0	0.0
2	1	12	56.0
2	2	25	116.7
2	3	10	46.7
2	4	13	66.7
2	5	6	28.0
3	1	1	4.8
3	2	4	19.0
3	3	6	28.5
3	4	2	9.5
3	5	1	4.8
4	1	15	80.0
4	2	8	42.7
4	3	2	16.7
4	4	4	21.3
4	5	1	5.3

estimate was 35.8.

No direct estimates of clerid departures were obtained. The available data suggest, however, that clerid arrivals exceeded departures during the early stages of southern pine beetle attack, but that this trend was reversed as time progressed. The mass attack of the southern pine beetle proceeded over the relatively short time span of 24 to 48 hours. The peak of clerid activity coincided with the mass attack period.

A single estimate of the number of southern pine beetles involved in a mass attack was obtained in the course of these investigations. An attacking population of 10,000 or more southern pine beetles was indicated from the data presented in Figure 6.

DISCUSSION

The impact of predators on prey populations has been the subject of considerable debate in the literature. It has been recognized that factors other than high prey consumption rate and high reproductive potential may be involved in determining predator effectiveness. Well adapted searching capacity, spatial and temporal synchrony, specialized behavioral patterns and the ability to survive at low prey densities can also be important determinants (Huffaker and Kennett, 1956).

Opinions regarding the effectiveness of Thanasimus dubius as a southern pine beetle predator have been mixed. Thatcher and Pickard (1966) concluded that T. dubius is not a highly efficient biological control agent for the southern pine beetle. They pointed to the lack of synchrony in predator and prey life cycles as well as activities on

alternate prey to substantiate this claim.

A countering opinion (Anonymous, 1972) suggested that the longer life span of T. dubius makes its predation more efficient and that the ability of the clerid to make use of alternate prey would be advantageous under endemic conditions when prey were scarce. Being capable of successfully reproducing on several prey species would enable the clerid to maintain a viable population that could respond immediately to the primary prey that suddenly increased in numbers.

Moore (1972) concurred with the latter opinion. He found that T. dubius was capable of responding to the southern pine beetle population density changes in a density dependent manner, and therefore, considered clerid predation of the southern pine beetle to be significant.

The present studies have found that T. dubius confines much of its activity to the southern pine beetle. The number of T. dubius active in southern pine beetle infestations exceeds that of Enoclerus nigripes. On the other hand, Berisford and Franklin (1972) found the reverse to be the case in studies of primary Ips infestations in four species of southern pine. These two studies would seem to indicate primary associations between T. dubius and D. frontalis, on the one hand, and between E. nigripes and certain Ips sp. on the other. Recent discoveries in the pheromone activities of the beetles involved may explain the relationships.

Vité and Williamson (1970) established that T. dubius follows aggregations of the southern pine beetle in response to pheromones released by that insect. They further determined that frontalin was the

component of the southern pine beetle pheromone complex triggering the response. The sensitivity of the clerid is apparently so developed that the compound can be detected at very low concentrations. Significantly, frontalin has not yet been implicated in the olfactory systems of other species of southern bark beetles.

The olfactory systems of three species of southern Ips have been worked out in part. Male Ips grandicollis have been found to initiate attacks on trees in response to olfactory stimuli of terpenes emanating from host trees (Werner, 1972a). Both sexes have been found to respond to a male-produced attractant found in the boring frass (Werner, 1972b). The attractant has been identified as Ipsenol (Anonymous, 1973). Ips calligraphus have been found to be guided by a combination of Ipsdienol and cis-verbenol (Renwick and Vité, 1972). This beetle also produces large quantities of trans-verbenol but that compound has not yet been implicated in attraction of the species. Ips avulsus has been reported to produce substantial quantities of Ipsdienol (Renwick and Vité, 1972).

The olfactory systems guiding aggregation of the southern pine beetle and the southern species of Ips seem to differ in the particular compounds eliciting response. Clerid predators are apparently capable of selectively responding to the compounds involved.

Thanasimus dubius has been reported active in Ips beetle infestations (Mignot and Anderson, 1969) and this would seem at odds with the theory proposed above. However, the clerid does respond to trans-verbenol (Vité and Williamson, 1970) which is released by a large variety of bark beetle species in contact with fresh, resinous host

material (Anonymous, 1972). The clerid also shows a low level of response to tree produced terpenes. These responses would seem sufficient to explain the presence of T. dubius in Ips infestations, especially in the absence of active southern pine beetle infestations. Hence, when populations of D. frontalis are low or the distribution of attractive centers scattered, the clerid might be expected to shift some of its predatory activity to alternative species.

Thanasimus dubius is apparently restricted to preying on members of the family Scolytidae. The limited range of suitable prey has been recognized as being general for clerids predatory on bark beetles (Struble, 1942; Berryman, 1970). Both the immature and adult stages of such species appear to be so restricted. To date, of the clerids known to prey on the Scolytidae, only Enoclerus lecontei has been reared successfully on a prey species from outside that family. Rice (1968) has succeeded in rearing several generations of that species on the cowpea weevil, Callosobruchus maculatus (Fabricius) (Coleoptera:Bruchidae).

The factors responsible for this phenomenon are poorly understood. Olfactory responses play a role in the general behavior of many clerids and visual and tactile stimuli can be observed as active in prey location, but the overall recognition sequence is yet to be examined. A sophisticated analysis of the sensory processes of clerids is needed to bridge the gap between ethological investigations and the work of the sensory physiologist.

Searching is an activity initiated by hunger and halted by satiation (Salt, 1967). Feeding history apparently determines a hunger threshold initiating searching activity by T. dubius but does not affect

prey utilization. Given the circumstance of successful prey location and capture, the clerid completely utilizes the prey as a food source.

Previous studies of prey consumption by adult T. dubius have been concerned with maximum and mean values and have not attempted to evaluate the effects of consumption on predator longevity and oviposition. Thatcher and Pickard (1966) determined that an adult T. dubius kills from 0 to 20 southern pine beetle adults per day with a mean value of 2.2. The maximum number of kills by an adult was 336. When prey availability exceeded the consumption rate, life spans of their clerids ranged from 35 to 74 days. They did not specify the sex, age and ovipositional status of the predators used in their studies, however.

Mignot and Anderson (1969) reported longevities of 21 to 57 days (mean at 25 °C was 51 days) for clerids fed a diet consisting largely of Ips grandicollis, but they did not record consumption rates.

It is important, however, to determine not only the maximum attainable longevity of a predator but also to consider longevity when prey population densities are at their lowest. How effective is the predator in overcoming periods when prey are scarce or unavailable?

The longevity of T. dubius adults is apparently determined by food availability. When clerids were subjected to conditions in which food was not limiting, prey consumption was determined by the physiological limits of satiation. Longevity under such conditions was largely independent of prey consumption, and therefore, a linear relationship existed between the time that predator and prey were exposed together and prey consumption. Berryman (1967 and 1970) reported similar findings for prey consumption by the larve of Enoclerus

lecontei. He found that the rate of predation on immature western pine beetles was not influenced by prey density in the field and attributed this to the fact that prey densities were rarely low enough to cause shortages.

When food became limiting, however, the longevity of T. dubius was largely determined by prey availability. Predator longevities below satiation feeding levels decreased with decreasing prey consumption, although the effects were not always directly correlated. Longevities for feeding schedules II through IV while progressively shorter were not significantly different, nor were those for schedules V and VI and schedules VII and VIII. The adult clerid is capable of not only a rather extended life span, but more significantly, is capable of exhibiting the long life over a relatively wide range of prey availability.

A functional response by adult T. dubius to changes in prey density was detected and is presented in Figure 20. Once the asymptote of the response curve was attained, however, prey availability no longer limited prey consumption and consumption was determined by available time. Under epidemic conditions and in light of the efficient prey location system available to the adult clerid, prey densities would seldom become limiting in the field. Predator activities under these conditions would be confined to those regions on the functional response curve beyond the asymptote. Mortality caused by the clerid would then become a function largely of predator density.

The clerid population active on a given tree apparently seldom exceeds 100 individuals at any point in time. Laboratory data presented
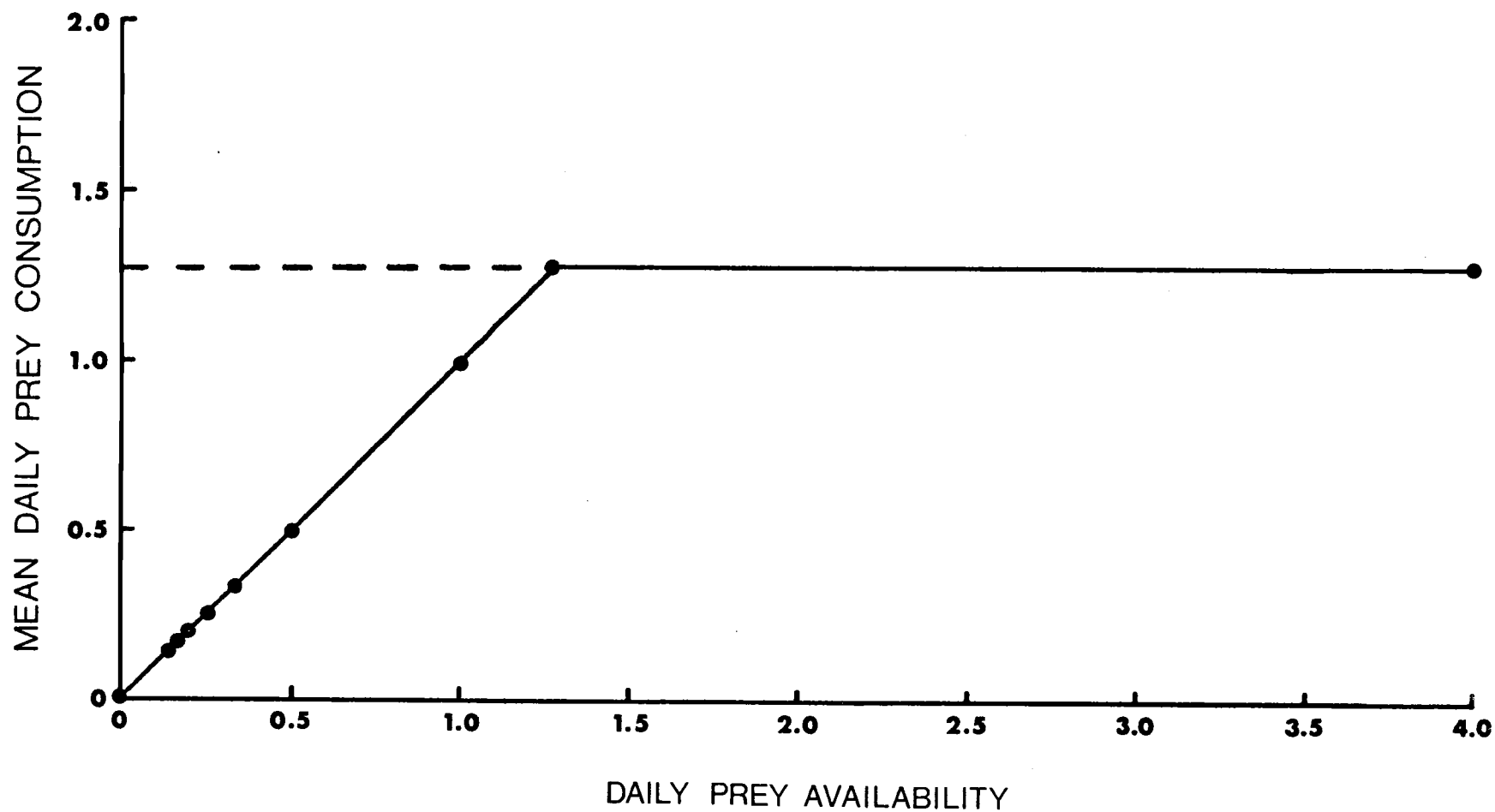
Figure 20. The functional response of individual adult _Thanasimus dubius_ Fabricius to changes in prey availability.

above indicate that effective predation by the adult clerids could average only about 1.2 prey per day for males and non-ovipositing females, and about 2.5 prey per day for ovipositing females. Assuming the sex ratio of the clerids on a tree to be one to one, total predation by 100 adult clerids would approximate 185 per day. Even if the maximum daily consumption rate oberved in these investigations could be sustained by all individuals, total predation could only approach 400 individuals per day. The significance of predation at such levels is open to question. It seems reasonable to assume, however, that predation by adult clerids operating with the population densities found here could not hope to prevent tree colonization. Observations by Franklin and Green (1965) tend to support this conclusion. They found that although attack density on a given tree undergoing mass attack might be significantly reduced by clerid predation, colonization and mortality of the tree still resulted.

Thatcher and Pickard (1966) found that oviposition by T. dubius varied from 0 to 44 per day, with a mean daily production of 2.4. The maximum number of eggs produced by a single female was 367. Mignot and Anderson (1969) reported oviposition ranging from 3.6 to 19.6 per week per female.

Chant (1961), however, has stated that the critical statistics in oviposition studies are not the maximum oviposition but the minimum prey consumption required for oviposition and the effects of prey consumption on oviposition rates. In my investigation mated T. dubius females did not oviposit when unfed. Mated females, however, with no previous history of oviposition or feeding were found to oviposit soon

after the consumption of one or two prey. Above the consumption threshold necessary to initiate oviposition, the oviposition rate was determined by the quantity of food ingested. Oviposition was significantly increased by increasing prey availability (and hence consumption) from 0.5 to 4.0 prey prey per day. Regression analysis of eggs produced per day against prey consumption indicated that oviposition was influenced mainly by prey consumption.

The number of eggs deposited per prey consumed was not changed by an increase in ovipositional activity. Oviposition increased directly with respect to prey consumption until an asymptote determined by the maximum possible prey consumption rate was attained. Oviposition on an infested tree, therefore, would be dependent to a degree on the density of the attacking southern pine beetle population and the ability of female clerids to locate and attack prey. In the presence of increasing prey populations, an increasing number of prey could be consumed and with this response the number of eggs produced per predator would be increased. This type of response would enable the clerid to make a numerical response with the next generation to changes in southern pine beetle density (Holling, 1959). This density-dependent reaction would operate only until the clerid reached its capacities for prey consumption and/or oviposition, and beyond these capacities prey density would be unaffected by predation or oviposition by the adult clerid.

The well developed host-finding mechanism of T. dubius together with its responsiveness to prey densities would seem to identify the clerid as an efficient predator. A distinction must be made, however,

between efficiency of predation and effectiveness as a control agent.
The functional (increase in the number of prey taken by an individual
predator) and numerical (increase in the reproductive capacity) re-
sponses identified in this study would make T. dubius responsive to
fluctuations in southern pine beetle population density. As a result
of these responses, the proportion of prey destroyed increases from
zero to some maximum prey density, and thereafter decreases. Thus,
predation by the clerid over some ranges of prey density shows a direct
density-dependent response and over others an inverse density-dependent
response. Under epidemic conditions adult T. dubius populations are
generally operating under the latter circumstance. The southern pine
beetle through its high reproductive rate and efficient population
aggregation methods is apparently capable of escaping the direct densi-
ty-dependent control of adult clerid predation. Clerid densities
present in the field are not normally high enough to compensate for
these two factors.

The role of the numerical response on the part of the clerid
is certainly important in the regulation of prey populations. The
full significance of increased predator reproduction with increased prey
density cannot yet be evaluated, however, as the impact of predation by
the larvae of T. dubius on immature southern pine beetle populations has
not been fully examined.

Populations of the southern pine beetle are undoubtedly regulated
by the interaction of many complex factors. In general, parasites and
predators cannot cause an epidemic of the pest to collapse before signi-
ficant damage has been done, because their response to increases in host

numbers is usually delayed. They are important pest regulators, how-
ever, and their role in the dynamics of prey populations warrants ef-
forts to preserve existing field populations. Forests can be managed
to maximize the effect of clerid predation on southern pine beetle
populations. Since the developing clerids emerge later than south-
ern pine beetle brood, discretion should be used in eliminating trees
at infestation sites. Trees already vacated by the southern pine
beetle brood should be left long enough for larval clerids to complete
development and emerge. Investigations into methods for preserving
predator populations by the use of selective control measures and
possibilities of increasing predator populations in epidemic conditions
by the release of laboratory-reared individuals should also be con-
sidered.

CONCLUSIONS

1. Adult Thanasimus dubius restrict their predatory activities to mem-
    bers of the family Scolytidae. Olfactory responses by the clerid
    further delimit these activities. Adult clerids are primarily found
    in association with the southern pine beetle, Dendroctonus frontalis.
2. The longevity of adult clerids is determined by food availability.
3. The sex, size and ovipositional status of the predator modify prey
    consumption rates. No effects of predator age on prey consumption
    could be demonstrated.
4. Oviposition is directly dependent on prey consumption. Oviposition
    in the field would be determined by the ability of females to

locate and capture prey.

5. Functional and numerical responses by adult T. <u>dubius</u> to changes in prey density have now been identified. These operate only at low prey densities, however, and under epidemic conditions the southern pine beetle is able to escape the density dependent controls of predation by the adult clerid.

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APPENDICES

TABLE XIII. DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 4.0
PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	74	♀	4.6	296	72
2	44	♂	4.3	176	64
3	75	♂	4.7	300	105
4	57	♀	4.8	228	54
5	79	♂	4.1	308	103
6	82	♀	4.7	328	88
7	38	♂	4.6	152	34
8	79	♂	4.5	308	92
9	38	♂	4.6	152	60
10	111	♀	4.8	444	145
11	122	♀	5.1	488	157
12	70	♂	4.5	280	85
13	102	♀	4.9	408	145
14	29	♂	4.9	116	22
15	96	♀	4.8	284	77
16	103	♀	4.9	412	237
17	66	♀	5.0	264	124
18	39	♂	4.3	156	93
19	102	♂	4.9	408	147
20	33	♂	4.3	132	48
21	125	♂	4.4	500	148

TABLE XIII. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
22	144	♂	4.3	576	141
23	192	♂	3.7	768	133
24	92	♂	4.4	368	70

TABLE XIV.   DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 1.0
             PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	99	♀	4.7	90	82
2	99	♀	4.8	90	84
3	56	♀	4.4	50	50
4	51	♂	4.6	48	41
5	71	♂	4.4	69	46
6	99	♀	5.2	98	85
7	66	♀	4.9	64	47
8	262	♀	5.0	250	242
9	46	♂	4.4	42	42
10	102	♀	4.7	92	89
11	165	♀	4.5	155	146
12	99	♂	4.5	90	82
13	43	♂	4.6	39	38
14	127	♀	4.3	117	113
15	93	♂	4.2	89	86
16	128	♀	4.7	120	118
17	122	♂	4.2	114	114
18	85	♂	4.6	80	78
19	127	♀	4.5	119	93
20	116	♀	4.5	110	104
21	73	♀	4.6	70	69
22	101	♀	4.8	98	90

TABLE XIV. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
23	42	♂	5.0	39	39
24	46	♂	4.9	43	37
25	49	♂	4.6	46	44
26	51	♀	4.7	48	44
27	88	♀	4.7	85	68
28	42	♂	4.6	40	32
29	48	♀	5.1	46	41
30	39	♀	5.0	38	35
31	53	♂	4.3	52	51
32	97	♀	4.5	94	89
33	65	♀	5.1	61	61
34	52	♀	5.1	49	48
35	75	♂	3.9	74	65
36	116	♀	5.0	115	112
37	49	♀	4.8	47	41
38	95	♀	4.8	94	94
39	164	♂	3.9	163	158
40	58	♀	4.5	57	57
41	64	♀	4.3	63	63
42	110	♀	4.3	109	108
43	146	♂	4.5	145	141
44	126	♂	4.7	125	124
45	91	♂	4.9	90	90

TABLE XIV. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
46	140	♀	4.6	139	138
47	229	♀	5.0	229	228
48	216	♂	4.3	216	213
49	141	♂	4.4	140	129
50	77	♀	4.5	76	75

TABLE XV.   DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 0.5
            PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	115	♀	4.8	57	57
2	32	♂	4.5	16	15
3	25	♂	4.8	12	12
4	86	♂	4.1	43	42
5	41	♀	4.4	21	21
6	84	♂	4.3	42	40
7	87	♀	5.0	43	42
8	60	♀	4.4	30	29
9	26	♀	5.2	13	12
10	59	♀	5.0	29	29
11	35	♂	5.0	17	17
12	49	♂	5.2	24	23
13	62	♂	4.6	31	29
14	39	♂	5.0	19	17
15	58	♀	5.1	29	28
16	63	♂	4.3	31	30
17	48	♂	4.5	24	24
18	51	♂	4.6	25	24
19	60	♀	4.1	30	30
20	38	♂	4.1	19	19
21	197	♀	4.7	98	98

TABLE XV. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
22	39	♂	4.8	19	19
23	37	♀	4.7	18	18
24	64	♀	4.7	32	31
25	73	♀	5.2	26	35
26	193	♂	4.4	96	96
27	55	♂	4.9	27	27
28	59	♂	4.5	29	29
29	68	♂	4.2	33	33
30	73	♀	4.8	36	36
31	236	♀	4.2	117	117
32	138	♀	5.0	69	68
33	135	♂	4.2	67	67
34	129	♀	3.7	65	62
35	34	♀	4.9	17	16
36	155	♂	3.6	78	70
37	110	♂	4.0	55	52
38	107	♂	4.6	53	52
39	103	♀	4.5	51	51
40	96	♂	4.3	48	46
41	180	♂	4.0	90	87
42	110	♀	3.9	55	54
43	87	♀	4.1	43	43

TABLE XV. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
44	109	♂	3.9	55	48
45	156	♂	3.8	78	73
46	150	♀	4.4	75	75
47	100	♀	5.5	50	49
48	130	♀	4.5	65	65
49	134	♂	4.6	67	66
50	62	♀	5.4	31	30

TABLE XVI. DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 0.33
            PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	137	♀	4.4	46	44
2	210	♂	4.8	70	69
3	103	♂	4.5	34	33
4	121	♀	4.5	40	40
5	147	♂	4.4	49	49
6	155	♀	4.8	52	51
7	121	♀	4.8	40	39
8	177	♀	5.0	60	60
9	40	♂	4.1	13	13
10	117	♂	5.0	39	39
11	190	♂	4.6	63	63
12	28	♀	5.5	9	9
13	52	♂	4.4	17	17
14	36	♀	5.4	12	12
15	52	♀	4.2	17	17
16	37	♂	4.7	12	12
17	43	♀	4.5	14	14
18	22	♂	4.0	7	7
19	38	♂	5.1	13	12
20	27	♂	5.0	9	8
21	67	♀	4.2	22	22
22	34	♀	4.5	11	11

TABLE XVI. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
23	38	♂	5.1	13	13
24	43	♀	4.7	14	14
25	49	♂	4.8	16	16
26	39	♀	4.7	13	13
27	71	♂	4.1	13	23
28	52	♂	4.9	17	16
29	160	♀	4.9	53	53
30	115	♀	4.8	38	37
31	202	♀	4.2	66	66
32	161	♂	3.9	54	53
33	96	♂	3.6	32	32
34	191	♂	4.6	64	63
35	131	♀	4.5	43	43
36	80	♀	4.5	27	26
37	130	♀	4.1	43	43
38	86	♀	4.5	29	29
39	168	♀	4.1	53	53
40	181	♀	4.8	61	60
41	126	♀	4.2	42	42
42	54	♀	3.9	18	15
43	27	♂	4.7	9	8
44	75	♂	4.6	25	24

TABLE XVI. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
45	54	♂	5.3	19	19
46	74	♀	5.2	26	25
47	133	♂	4.5	45	45
48	61	♂	5.3	21	21
49	83	♀	4.5	28	28
50	68	♂	4.6	22	21

TABLE XVII. DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 0.25
PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	76	♂	5.0	19	19
2	72	♀	5.1	18	18
3	32	♂	4.4	8	8
4	62	♀	4.5	15	15
5	70	♀	5.5	17	17
6	28	♀	5.4	7	7
7	33	♂	4.2	8	8
8	31	♂	4.4	7	6
9	36	♂	4.7	9	9
10	27	♀	4.5	7	7
11	71	♀	5.4	18	18
12	53	♀	5.0	15	14
13	37	♀	4.8	9	8
14	44	♂	4.5	11	10
15	30	♀	5.0	8	7
16	31	♂	5.2	7	7
17	36	♀	5.0	9	9
18	31	♂	4.9	7	7
19	42	♀	4.7	10	10
20	18	♂	4.8	5	4
21	36	♀	4.9	9	9

TABLE XVII. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
22	26	♂	4.7	6	6
23	38	♀	5.0	10	9
24	31	♀	4.5	8	8
25	33	♀	4.8	9	8
26	27	♀	4.4	7	7
27	21	♂	4.1	5	5
28	61	♀	4.5	15	15
29	134	♂	5.0	34	34
30	78	♀	3.9	20	18
31	93	♀	4.9	23	23
32	20	♀	4.8	5	5
33	27	♂	4.8	7	7
34	38	♀	4.1	10	8
35	57	♀	5.9	14	14
36	64	♀	5.5	16	16
37	57	♀	4.5	14	14
38	50	♂	5.1	13	12
39	79	♂	4.2	20	20
40	62	♂	5.6	16	16
41	55	♀	4.7	14	14
42	60	♂	5.5	15	15
43	26	♂	3.8	7	6
44	45	♂	5.0	11	11

TABLE XVII. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
45	44	♀	4.9	11	11
46	31	♂	5.0	8	8
47	28	♂	4.2	7	7
48	73	♀	4.5	18	18
49	74	♀	4.4	18	18
50	67	♂	5.0	17	17

TABLE XVIII.   DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 0.20
               PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	37	♂	4.7	8	7
2	36	♂	5.0	7	7
3	56	♀	5.2	11	11
4	19	♀	4.6	4	4
5	51	♀	4.7	10	10
6	22	♂	5.0	5	5
7	30	♂	4.9	6	6
8	34	♂	4.2	7	7
9	21	♂	4.7	4	4
10	21	♂	4.9	4	4
11	34	♂	4.2	7	6
12	52	♀	5.3	11	19
13	23	♀	4.7	5	5
14	26	♀	5.0	5	5
15	30	♀	4.3	6	5
16	30	♀	4.8	6	5
17	36	♀	4.9	7	6
18	35	♀	4.5	7	6
19	27	♀	4.3	6	5
20	27	♂	4.1	6	5
21	112	♀	4.5	23	22
22	52	♂	3.9	11	10

TABLE XVIII. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
23	66	♀	4.4	13	13
24	135	♀	4.3	27	27
25	40	♂	4.4	9	9
26	35	♂	4.3	8	8
27	36	♂	4.5	9	8
28	94	♂	4.2	20	20
29	92	♀	4.0	19	19
30	49	♂	4.3	10	9
31	32	♀	4.4	7	6
32	88	♀	4.3	18	17
33	52	♀	5.5	10	10
34	27	♀	5.5	6	6
35	46	♂	5.2	9	9
36	49	♂	4.7	10	10
37	46	♀	4.6	10	10
38	24	♂	4.1	5	5
39	51	♀	4.2	10	10
40	46	♂	4.0	9	9
41	44	♀	4.2	9	9
42	51	♀	4.7	10	10
43	26	♀	4.5	5	4
44	46	♂	4.9	9	9

TABLE XVIII. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
45	39	♂	4.1	8	8
46	25	♂	4.5	5	5
47	95	♂	4.1	19	18
48	36	♂	4.4	7	6
49	52	♂	4.4	11	10
50	56	♂	5.0	11	11

TABLE XIX.   DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 0.17
             PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	28	♂	4.9	5	5
2	26	♂	4.4	4	4
3	28	♂	4.8	5	5
4	49	♀	5.5	8	8
5	22	♂	4.3	4	4
6	48	♂	4.7	8	8
7	26	♂	4.5	5	5
8	28	♀	4.9	5	5
9	33	♀	4.9	6	6
10	24	♀	5.0	4	4
11	42	♂	5.0	7	7
12	48	♀	5.3	8	8
13	27	♂	4.4	5	5
14	22	♂	4.2	4	4
15	15	♀	4.9	3	3
16	22	♀	4.4	4	4
17	22	♀	5.5	5	4
18	20	♀	4.6	4	4
19	26	♀	5.3	5	5
20	20	♀	5.3	3	3
21	20	♀	5.0	3	3

TABLE XIX.   (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
22	22	♀	5.1	4	3
23	20	♀	4.8	3	3
24	20	♂	4.0	3	3
25	38	♀	5.0	6	6
26	13	♂	4.9	2	2
27	25	♂	5.0	3	3
28	22	♂	4.4	4	3
29	28	♂	4.6	5	5
30	18	♂	5.2	3	3
31	20	♀	4.8	4	4
32	20	♀	4.4	4	4
33	15	♂	4.3	5	4
34	38	♀	5.1	5	5
35	27	♀	4.8	5	5
36	30	♀	4.4	5	5
37	15	♂	4.2	3	3
38	18	♂	4.6	3	3
39	24	♂	4.4	4	4
40	24	♀	5.0	4	4
41	38	♀	5.0	7	6
42	36	♂	4.7	6	6
43	30	♂	4.2	5	5
44	28	♂	4.2	5	5

TABLE XIX.   (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
45	26	♀	4.7	6	6
46	33	♀	5.2	6	5
47	34	♂	5.1	6	6
48	34	♀	5.0	6	6
49	104	♀	3.7	18	18
50	35	♂	4.4	6	6

TABLE XX. DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 0.14
PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	43	♂	4.3	6	6
2	47	♀	5.6	7	7
3	38	♀	4.9	6	6
4	49	♂	4.7	7	7
5	35	♂	4.3	5	5
6	32	♀	5.0	5	5
7	32	♂	4.6	5	5
8	16	♀	4.3	3	3
9	14	♂	4.2	2	2
10	13	♀	4.9	2	2
11	15	♂	4.5	2	2
12	23	♂	4.4	4	4
13	31	♀	4.5	5	5
14	43	♀	5.0	6	6
15	24	♀	4.5	4	4
16	21	♀	5.0	3	3
17	24	♂	4.0	4	3
18	14	♂	4.8	2	2
19	19	♀	4.3	3	3
20	35	♀	4.9	5	5
21	20	♂	4.7	3	3
22	19	♂	4.9	3	3

TABLE XX. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
23	26	♀	3.9	3	3
24	26	♀	4.7	4	4
25	26	♀	4.5	4	4
26	24	♂	3.9	3	3
27	44	♀	3.6	7	7
28	35	♀	4.8	5	5
29	39	♀	4.3	6	6
30	29	♂	4.6	4	4
31	18	♂	5.0	3	3
32	26	♂	4.3	4	4
33	15	♀	5.0	2	2
34	30	♂	4.9	5	4
35	35	♀	4.8	5	5
36	30	♀	5.0	5	4
37	15	♀	4.8	2	2
38	21	♀	5.2	3	3
39	22	♂	4.7	3	3
40	21	♀	4.9	3	3
41	15	♀	4.9	2	2
42	15	♂	4.7	2	2
43	21	♀	5.0	3	3
44	38	♀	4.4	6	5
45	14	♂	4.7	2	2

TABLE XX.   (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
46	22	♂	3.8	3	3
47	34	♀	4.7	5	5
48	24	♀	4.3	4	3
49	38	♂	5.3	6	6
50	22	♂	4.2	3	3
51	43	♀	5.0	6	6

TABLE XXI. DATA SUMMARIES FOR INDIVIDUAL CLERIDS RECEIVING 0.0
            PREY PER DAY

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
1	11	♂	4.5	0	0
2	27	♀	4.8	0	0
3	18	♀	4.9	0	0
4	13	♀	4.6	0	0
5	10	♂	4.6	0	0
6	11	♂	4.8	0	0
7	12	♂	4.3	0	0
8	18	♀	4.1	0	0
9	20	♀	4.0	0	0
10	14	♀	4.3	0	0
11	13	♂	4.5	0	0
12	13	♀	4.2	0	0
13	10	♂	4.0	0	0
14	14	♂	4.7	0	0
15	13	♂	4.6	0	0
16	19	♂	4.8	0	0
17	18	♀	4.3	0	0
18	12	♂	4.3	0	0
19	15	♀	4.3	0	0
20	17	♂	4.2	0	0
21	17	♂	4.3	0	0
22	17	♀	4.3	0	0

TABLE XXI. (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
23	13	♂	4.7	0	0
24	16	♂	4.4	0	0
25	18	♀	4.8	0	0
26	9	♂	4.1	0	0
27	16	♀	4.2	0	0
28	15	♀	4.9	0	0
29	16	♂	4.5	0	0
30	16	♂	4.6	0	0
31	14	♀	4.9	0	0
32	25	♀	5.1	0	0
33	37	♂	4.6	0	0
34	23	♂	4.7	0	0
35	17	♂	5.2	0	0
36	24	♂	4.8	0	0
37	18	♂	4.1	0	0
38	20	♀	5.0	0	0
39	26	♂	4.4	0	0
40	23	♀	4.4	0	0
41	12	♀	4.8	0	0
42	15	♀	4.0	0	0
43	16	♂	5.0	0	0
44	16	♂	5.0	0	0

TABLE XXI.   (CONTINUED)

Clerid Number	Longevity (days)	Sex	Elytral Length (mm)	Number of Prey Offered	Number of Prey Consumed
45	23	♀	5.2	0	0
46	19	♂	4.9	0	0
47	25	♂	4.6	0	0
48	16	♀	4.7	0	0
49	28	♀	4.7	0	0

TABLE XXII. PREY UTILIZATION BY ADULT MALE THANASIMUS DUBIUS FABRICIUS

Prey Number	Prey Live Weight (grams)	Prey Dead Weight (grams)	Net (grams)	Percent Consumed
1	0.0021	0.0004	0.0017	80.95
2	0.0025	0.0006	0.0019	76.00
3	0.0024	0.0006	0.0018	75.00
4	0.0024	0.0003	0.0021	87.50
5	0.0016	0.0004	0.0012	75.00
6	0.0016	0.0005	0.0011	68.75
7	0.0018	0.0003	0.0015	83.33
8	0.0023	0.0004	0.0019	82.61
9	0.0022	0.0004	0.0018	81.82
10	0.0029	0.0004	0.0025	86.21
11	0.0018	0.0004	0.0014	77.78
12	0.0019	0.0004	0.0015	78.95
13	0.0022	0.0004	0.0018	81.82
14	0.0032	0.0007	0.0025	78.13
15	0.0019	0.0004	0.0015	78.95
16	0.0017	0.0003	0.0014	82.35
17	0.0037	0.0009	0.0028	75.68
18	0.0027	0.0005	0.0022	81.48
19	0.0034	0.0006	0.0028	82.35
20	0.0029	0.0008	0.0021	72.41
21	0.0034	0.0007	0.0027	79.41
22	0.0025	0.0004	0.0021	84.00

TABLE XXII. (CONTINUED)

Prey Number	Prey Live Weight (grams)	Prey Dead Weight (grams)	Net (grams)	Percent Consumed
23	0.0035	0.0007	0.0028	80.00
24	0.0030	0.0008	0.0022	73.33
25	0.0038	0.0007	0.0031	81.58
26	0.0026	0.0006	0.0020	76.92
27	0.0031	0.0007	0.0024	77.42
28	0.0035	0.0004	0.0031	88.57
29	0.0024	0.0007	0.0017	70.83
30	0.0030	0.0006	0.0024	80.00
31	0.0029	0.0005	0.0024	82.76
32	0.0029	0.0005	0.0024	82.76
33	0.0022	0.0002	0.0020	90.91
34	0.0028	0.0004	0.0024	85.71
35	0.0028	0.0006	0.0022	78.57
36	0.0028	0.0006	0.0022	78.57
37	0.0024	0.0008	0.0016	66.67
38	0.0025	0.0003	0.0022	88.00
39	0.0028	0.0005	0.0023	82.14
40	0.0030	0.0007	0.0023	76.67
41	0.0013	0.0001	0.0012	92.31
42	0.0012	0.0003	0.0009	75.00
43	0.0027	0.0004	0.0023	85.19
44	0.0030	0.0006	0.0024	80.00

TABLE XXII. (CONTINUED)

Prey Number	Prey Live Weight (grams)	Prey Dead Weight (grams)	Net (grams)	Percent Consumed
45	0.0018	0.0002	0.0096	88.89
46	0.0023	0.0004	0.0019	82.60
47	0.0026	0.0008	0.0018	69.23
48	0.0036	0.0006	0.0030	83.33
49	0.0018	0.0005	0.0013	72.22
50	0.0027	0.0006	0.0021	77.78

TABLE XXIII.   PREY UTILIZATION BY ADULT FEMALE <u>THANSIMUS</u> <u>DUBIUS</u> FABRICIUS

Prey Number	Prey Live Weight (grams)	Prey Dead Weight (grams)	Net (grams)	Percent Consumed
1	0.0024	0.0007	0.0017	70.83
2	0.0023	0.0005	0.0018	78.26
3	0.0020	0.0006	0.0014	70.00
4	0.0018	0.0003	0.0015	83.33
5	0.0023	0.0004	0.0019	82.61
6	0.0021	0.0003	0.0018	85.71
7	0.0015	0.0002	0.0013	86.67
8	0.0018	0.0002	0.0016	88.89
9	0.0018	0.0003	0.0015	83.33
10	0.0022	0.0004	0.0018	81.82
11	0.0021	0.0004	0.0017	80.95
12	0.0019	0.0002	0.0017	89.47
13	0.0015	0.0005	0.0010	66.67
14	0.0022	0.0003	0.0019	86.36
15	0.0023	0.0006	0.0017	73.91
16	0.0025	0.0005	0.0020	80.00
17	0.0029	0.0007	0.0022	75.86
18	0.0036	0.0006	0.0030	83.33
19	0.0033	0.0008	0.0025	75.76
20	0.0032	0.0009	0.0023	71.87
21	0.0030	0.0009	0.0021	70.00
22	0.0024	0.0005	0.0019	79.17

TABLE XXIII. (CONTINUED)

Prey Number	Prey Live Weight (grams)	Prey Dead Weight (grams)	Net (grams)	Percent Consumed
23	0.0029	0.0006	0.0023	79.31
24	0.0026	0.0007	0.0019	73.08
25	0.0026	0.0007	0.0019	73.08
26	0.0028	0.0007	0.0021	75.00
27	0.0026	0.0008	0.0018	69.23
28	0.0027	0.0005	0.0022	81.48
29	0.0038	0.0005	0.0033	86.84
30	0.0018	0.0003	0.0015	83.33
31	0.0025	0.0003	0.0022	88.00
32	0.0020	0.0003	0.0017	85.00
33	0.0026	0.0004	0.0022	84.62
34	0.0033	0.0005	0.0028	84.85
35	0.0026	0.0003	0.0023	88.46
36	0.0028	0.0005	0.0023	82.14
37	0.0026	0.0006	0.0020	76.92
38	0.0037	0.0006	0.0031	83.78
39	0.0022	0.0005	0.0017	77.27
40	0.0022	0.0003	0.0019	86.36
41	0.0025	0.0009	0.0016	64.00
42	0.0021	0.0004	0.0017	80.95
43	0.0027	0.0005	0.0022	81.48
44	0.0031	0.0007	0.0024	77.42

TABLE XXIII. (CONTINUED)

Prey Number	Prey Live Weight (grams)	Prey Dead Weight (grams)	Net (grams)	Percent Consumed
45	0.0030	0.0004	0.0026	86.67
46	0.0036	0.0008	0.0028	77.78
47	0.0025	0.0005	0.0020	80.00
48	0.0024	0.0008	0.0016	66.67
49	0.0029	0.0008	0.0021	72.41
50	0.0021	0.0005	0.0016	76.19