LIFE HISTORY ENERGETICS OF THE RED-EARED TURTLE,
PSEUDEMYS SCRIPTA, IN NORTH CENTRAL TEXAS

DISSERTATION

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DOCTOR OF PHILOSOPHY

by

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A population of the red-eared slider, <u>Pseudemys</u>
<u>scripta</u>, in north central Texas was studied from 1975
to 1980. A life history energy budget was developed for
a typical individual in the population and the population
dynamics were estimated.

A growth model relating growth rate to mean plastron
length (PL) was developed from recapture data and used to
1) establish age classes and 2) age individuals. Growth
rate was highly variable in both sexes. Females grew more
rapidly than males and attained a larger maximum size
(230 mm and 195 mm PL in females and males respectively).

Females reached sexual maturity in their ninth year
at a PL of 185-190 mm. Males matured in their sixth year
at a PL of 90-100 mm. Females produced three clutches
annually; clutch size ranged from 7 to 14 (X=10.3; N=20).
Ova were enlarged in the early spring and ovulation began
in late April and early May. Egg laying occurred from mid-
May through June. Both egg size and clutch size increased
with female body size.

Lipid levels were variable within and among seasons.

No annual lipid cycling pattern was evident in females. The proportion of assimilated energy devoted to reproduction, a measure of reproductive effort (RE), by females, was 13 per cent the first year of maturity (9 y) and increased to 20 per cent by their twentieth year. Lifetime RE was 16 per cent.

Population density was estimated as 51 males and 50 females per ha in a 8.2-ha area of the lake. Young juveniles (less than 2 y) were not present although other subadult age classes were about equally represented. Fewer adults were encountered. An annual total production of 4000 eggs was estimated for the population present in 1977. A survival rate of from 2 to 18 per cent was estimated for the period between egg laying to 3 y. The large group of turtles younger than 10 y represented an expanding (R_o=1.8) lake population and the small group of older turtles were the remanants of a creek population present before Moss Lake was formed.

The demographic environment, high juvenile mortality and low adult mortality, was suggested as a primary selective force shaping the life history characteristics of the Moss Lake P. scripta population.

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CHAPTER I

INTRODUCTION

During the past two decades theoretical literature on the evolution of life history traits (e.g., Williams 1966 a,b; MacArthur and Wilson 1967; Murphy 1968; Pianka 1970, 1972; Tinkle 1969; Tinkle et al. 1970; Wilbur et al. 1974; Hirschfield and Tinkle 1975; Stearns 1976, 1977) has focused on reproductive tactics. Many workers (e.g. Fitzpatrick 1972; Tinkle and Hadley 1975; Pianka and Parker 1975; Congdon et al. 1978; Dial and Fitzpatrick 1981) have addressed the central question posed over 50 years ago by R.A. Fisher (1930): "It would be instructive to know not only by what physiological mechanism a just apportionment is made between nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life history and environment would render profitable the diversion of a greater or lesser share of the available resources toward reproduction." It is necessary to study those selective factors that influence when and how much of an organism's available resources should be devoted to reproduction in order to understand the adaptive significance of life-history patterns of reproduction.

Resource level and demographic environment have been suggested as two primary selective factors influencing reproductive strategies. The resource level theory (r and K-selection) predicts that organisms having high per capita resource levels will evolve a set of traits (r-selection): early maturity, high fecundity, small offspring, short life expectancy and high reproductive effort. Organisms existing under low per capita resource levels will develop an alternate set of traits (K-selection): late maturity, low fecundity, large offspring, long life expectancy and low reproductive effort (Dobzhansky 1950; MacArthur and Wilson 1967; Pianka 1970, 1972).

Williams (1966a,b) proposed that the demographic environment is a selective factor in the evolution of reproductive tactics, and that a given reproductive effort is a function of current and future reproductive value. Accordingly, Williams predicted (1) that long-lived species should commit fewer resources to reproduction per breeding season than short-lived species, and (2) within a species reproductive effort should increase with age as a function of declining life expectancy or future breeding opportunities. Others (e.g., Murphy 1968; Hirschfield and Tinkle 1975; Stearns 1976, 1977) have emphasized more stochastic demographic factors such as the relation between juvenile and adult survivorship, as selective factors.

Similar sets of life history characteristics are predicted as the result of different selective forces (Wilbur, Tinkle and Collins 1974). Low reproductive effort and long life expectancy are predicted both by the r and K theory and the demographic environment theory. However, as pointed out by Congdon and Tinkle (1982), stored energy in the form of lipids may respond differently to alternate selective forces. The timing and magnitude of reproduction are somewhat separated from immediate ecological conditions by the use of stored body lipids. Energy harvested at times when food is more available or more easily obtained can be stored in the form of lipids, then diverted to reproductive tissues (yolk material, sperm, etc.) or energy production for reproductive activities (nesting, courtship), at a time more favorable to reproduction. Congdon and Tinkle (1982) predicted that (1) in a competitive environment where resources are limiting (K-selection), storage levels should not fluctuate dramatically, compared to reproductive output, in response to an increase in resource availability, and (2) in contrast, in environments where juvenile mortality is high and unpredictable, an increase in resources should cause an increase in stored lipids rather than an increase in reproductive output.

Testing and refining life history theory requires more comparative data on the relation of reproductive tactic

(reproductive effort) and the ecological and demographic history of populations. Data on long-lived organisms are especially needed.

Many turtles possess a unique set of life history traits and should represent a valuable group for comparison. Most turtle species are among the longest-lived vertebrates, yet exhibit rather uncomplicated life history patterns. Once sexual maturity is obtained, turtles essentially are annual breeders, producing discrete clutches of eggs and providing no post-nesting parental care. This simple reproductive pattern allows for a reasonably direct measurement of reproduction. The number of eggs and chemical energy invested in the egg mass, can be measured relatively easily and constitute a reasonable measure of reproduction. Thus, the complications in measuring the energy supplied to the post-embryonic offspring by the parents, and the energy expended by the parents in obtaining such, that are encountered in measuring reproductive effort in most long-lived animals (i.e., birds and mammals) are avoided in turtles.

Many aspects of the natural history of North American fresh water turtles are known (Ernst and Barbour 1972, Harless and Morlock 1979). However, as stressed by Bury (1979), the population dynamics of fresh water turtles are poorly known; the information necessary to understand the

role turtles play in community energy flow, to understand
their response to and ability to withstand environmental
changes, and to make wise decisions concerning management is
wholly inadequate.

The red eared turtle, Pseudemys scripta (Schoepff), was
chosen as a study animal for several reasons. It is
frequently the most abundant turtle within its habitat, is
easily observed and trapped in large numbers, and can be
readily maintained under laboratory conditions. Because of
its abundance and durability, P. scripta has been the
subject of a considerable number of life history and
ecological studies. Consequently a large body of information
is available concerning its natural history (Cagle
1946,1950; Carr 1952; Moll and Legler 1971; Ernst and
Barbour 1972), and reproductive and population dynamics
(Gibbons 1970a, Gibbons et al. 1981, Thornhill 1982). Yet
little is known of energy partitioning in P. scripta.

This study concerns life history energetics and
population dynamics of a P. scripta population in north
central Texas. Specific objectives were to determine

(1) the annual age-specific energy budget, the
partitioning of energy among maintenance,
storage, growth, and reproduction of a typical
individual;

(2) the life history energy budget of an individual
from the egg through the maximum life span (Are
levels of reproductive effort, RE, measured as a
proportion of available energy, lower in P.
scripta than in short-lived species? Does RE
increase with age?);

(3) the relation of lipid storage and utilization to
reproduction (Is lipid cycling related to
reproduction? Is the quantity of stored lipids
more variable than reproductive output?);

(4) the energy flow within the population (What is
the population size? Is the population size
stable? How much energy flows through the
population?);

(5) the survivorship and fecundity schedules (What is
the demographic environment?).

CHAPTER II

SPECIES STUDIED

The red-eared slider, _Pseudemys scripta_, is one of the most widely distributed North American freshwater turtle species, ranging from Illinois and Indiana south through most of the southeastern United States and Texas to northern South America (Pritchard 1967). _P. scripta_ has a broad ecological tolerance, occurring in almost all freshwater habitats. Preferred habitats include quiet water with abundant aquatic vegetation and emergent basking sites.

A wide range of food items has been recorded in the diet of _P. scripta_, including algae and assorted herbaceous plants. There is an ontogenetic change in feeding tactics from carnivory in juveniles to omnivory in adults (Clark and Gibbons 1969, Parmenter 1980, Hart 1983). Clark and Gibbons (1969) suggested that the carnivorous diet of juveniles provides protein and calcium necessary for rapid growth and shell formation, while an opportunistic omnivorous diet of larger individuals allows reduced energetic cost of feeding and consequently survival in a wider range of habitats.

P. scripta are diurnal, feeding and basking during the day and sleeping on the bottom or on submerged surfaces,

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such as brush piles, during the night. Aerial basking is well developed. Sliders frequently congregate on suitable basking sites such as emergent logs. During spring and fall, times when air temperature and insolation allow turtles to raise their body temperature above the water temperature (Boyer 1965), sliders spend considerable time basking.

The sexes are highly dimorphic and easily distinguished after 2 y of age. Adult males are smaller with a relatively flattened carapace and have elongated foreclaws and an enlarged precloacal area which places the cloacal opening posterior to the carapacial margin. Males frequently become darker with age as melanin deposits increase.

CHAPTER III

THE STUDY SITE

H.H. Moss Reservoir is a 455-ha impoundment located 16 km NW of Gainesville, Cooke County, in north central Texas (Figure 1). Moss Lake, constructed in 1966 as a municipal and industrial water source, is within the Red River drainage and has a 168 km^2 drainage basin. The mean depth is 6.03 m, maximum depth is 20 m (Boswell 1977). The surface area with water depth of less than 5 m includes 141 ha (30.6 per cent). Moss Lake consists of two major branches, North Fish Creek and South Fish Creek. In the distal end of each branch and in small creeks and coves around the lake there are numerous emergent tree stumps and logs which provide abundant basking sites. Aquatic vegetation, primarily Potomogeton sp., is also abundant in shallow areas throughout the lake. Water lilies (Nymphaea) are common in South Fish Creek and adjacent shallow areas of the lake, forming dense mats of floating leaves. P. scripta is the most abundant turtle species. Only two other turtle species were observed, the spiny softshell (Trionyx spiniferus) and the snapping turtle (Chelydra serpentina).

Figure 1. Location of H. H. Moss Reservoir. The
stippled area indicates area of water depth
less than 5 m. The mark and recapture area
is enclosed by a dashed line. Figure drawn
from United States Geological Survey topo-
graphic maps (7.5 minute series; 1:24,000).

Figure 1
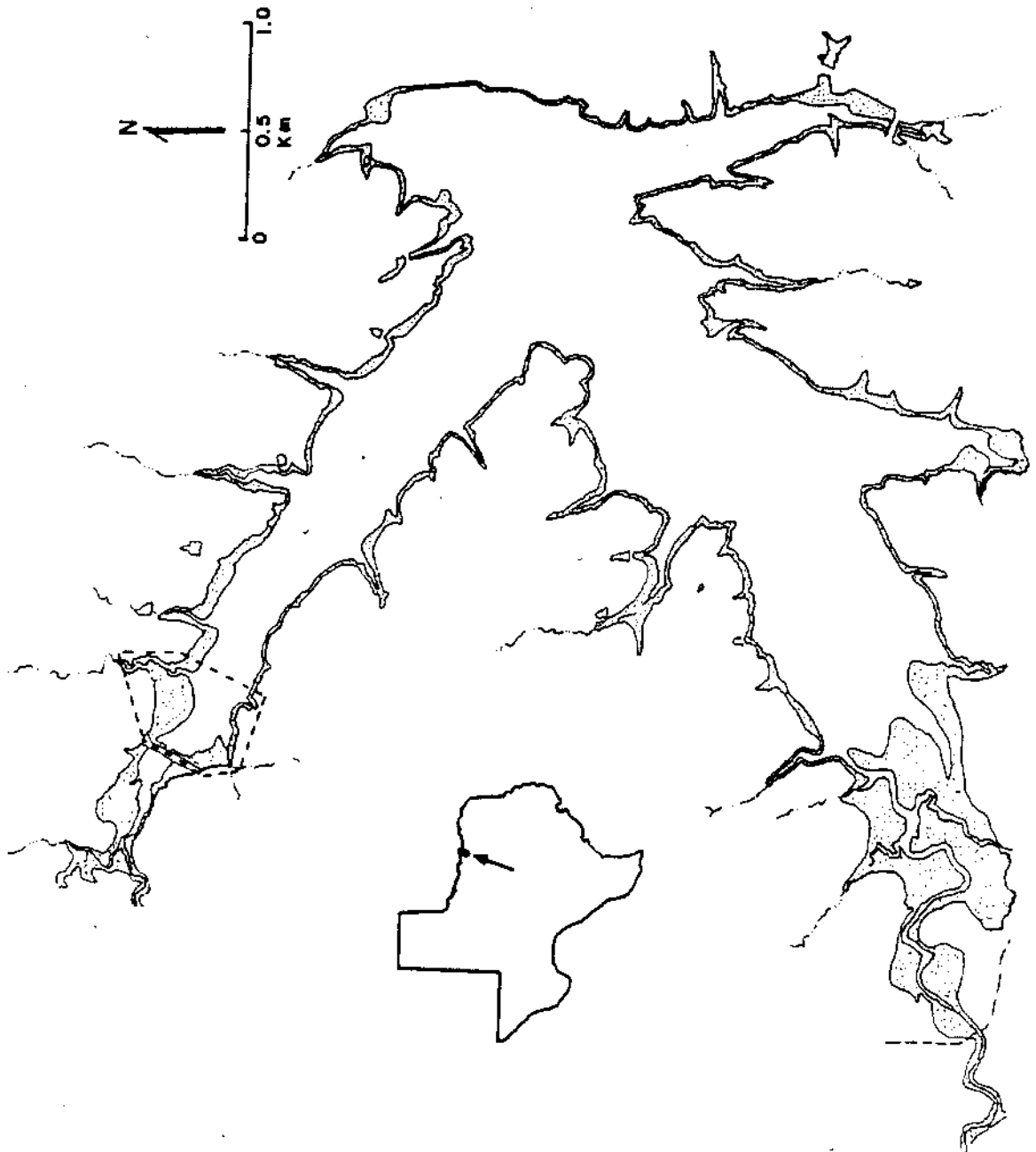
The distal end of the North Fish Creek branch of the lake was chosen as a mark and release area (Figure 1) and includes a surface area of 8.2 ha, 5.2 ha of which has a water depth of less than 5 m. The mark and release area is apparently an area turtles prefer over other areas in the lake. This is an area of relatively shallow water, partly separated from the lake by a narrow peninsula. Due to the partial separation, the relief of the surrounding terrain, and the prevailing winds, wave action affects this area less than most other parts of the lake. The abundance of emergent basking sites and aquatic vegetation, and calmer water, seems to attract turtles.

CHAPTER IV

MATERIALS AND METHODS

Age Determination

Age in long-lived turtles is difficult to determine
during relatively short-term studies (Gibbons 1976).
Generally, growth rings on epidermal scutes are used to
estimate age (Sexton 1959a, Legler 1960, Gibbons, 1968).
Unfortunately, annuli become obscure after a few years in
larger individuals in P. scripta from Moss Lake. Because
external annuli could not be used to age older (mature)
individuals, a method applicable to all age classes based on
growth rates of marked individuals was used to develop an
age-size relationship.

From May 1977 through May 1980, turtles were trapped
from various sites around Moss Lake where water depth was
less than 5 m. Trapping was concentrated in two large areas:
(1) the west end of the lake, approximately 100 m of South
Fish Creek and two shallow coves connected to this portion
of the creek, and (2) the distal end of the North Fish Creek
arm of the lake (Figure 1).

Turtles were collected exclusively in baited funnel
traps set on the bottom. Traps were constructed from 2.5-cm

mesh poultry wire, and were 0.3 m high, 0.5 m wide and 1 m long. The ends were constructed to form a funnel with a narrow horizontal opening slightly less than the width, a design facilitating dorso-ventrally compressed turtles entering traps but discouraging laterally compressed fish. Bait was primarily chopped fresh fish, but also included chicken necks and fat, canned sardines, canned dog food and various road-killed animal carcasses.

Traps were set near areas where turtles were frequently seen, such as log piles with submerged retreats and emergent basking sites, or preferred foraging areas, such as dense stands of submerged vegetation. No attempt was made to trap uniformly throughout an area. Traps were generally set in the morning, checked at 2 3-h intervals and removed before sunset. The time that traps were in place was recorded, but no attempt was made to standardize trap-hours per time period. The spacing of the traps and the timing of trapping periods were designed to maximize the number of turtles collected rather than to define turtle distribution or activity.

With the exception of one sample of turtles, which was returned to the laboratory and released 3 days later, turtles were processed in a temporary lab at the lake and released near the area where traps were set within 8 h. Turtles collected for the first time were marked

individually, and the identification of recaptured turtles was recorded. Turtles were marked either by hot-branding numerals in the abdominal or femoral scutes or by sawing notches in the peripheral edges of plastral scutes into the underlying bone. Branding was unsatisfactory for permanent identification, due to distortion of the branded numerals as scutes increased in size, and was discontinued. The notching method was more reliable, and notches were distinct after 3 y. No permanent damage was known to occur from either brands or notches.

Plastron length (PL) and carapace length (CL) were measured to the nearest mm with large, specially constructed, callipers. Lengths of annuli present on the right pectoral scute were measured to the nearest 0.1 mm with a Vernier calliper. Turtles were weighed to 0.1 g on an Ohaus triple-beam balance with a specially curved pan. Female turtles were palpated to determine the presence of eggs in the oviducts.

The growth model used is a permutation (Van Devender 1975) of the Von Bertalanffy general growth model (Von Bertalanffy 1951, 1957) in which growth rate is assumed to be a linear function of body size. Daily growth rate (GR), measured as change in PL between captures divided by the number of activity days (see comments below) between captures, was treated as a dependent variable in a simple

linear regression with mean PL (MPL) between captures as the independent variable:

$$GR = a + b\ MPL \qquad (1)$$

This regression equation was treated as a differential equation and integrated to relate size and age (Van Devender 1975):

$$Age_x = 1/b\ log_e\ (a * b\ PL) + c \qquad (2)$$

where a and b are the intercept and slope, respectively, of equation 1 and c is an integration constant. The value of c can be determined if age at any size is known.

Metabolic Heat Loss

The relation between energy lost as metabolic heat and environmental temperature was measured indirectly by O_2 consumption ($\dot{V}O_2$) in turtles taken from Moss Lake during the spring and summer of 1978 when water temperature was approximately 10, 15, 20, 25, and $30^O C$, respectively. Water temperature at 1 m depth in an area where turtles frequently basked was measured continuously from February 1977 to July 1978 by a Bacharach recording thermometer. Water temperatures taken at each trap site were generally the same and always $\pm$ $2^O C$ of the recorded temperature on any

particular day. Turtles in these five collections were considered to be field-acclimatized to the prevailing water temperature. Each group was maintained in the laboratory at its acclimatization temperature (AT) for 7-15 days without food in a 1.2 x 2.4 x 0.4 m water bath and under natural photoperiod.

Oxygen consumption was measured in constant volume manometric respirometers constructed of two equal size vessels, a respiration chamber and a compensating thermobarometer, connected via rubber tubing to a manometer U-tube partially filled with Brody's fluid. Four sizes of respiration vessels (2, 3, 4, and 8 l) were used to keep body volume/vessel volume ratios similar over the size range of the turtles. A 10 per cent KOH solution was used to absorb CO_2 in both vessels. Vessels were maintained in a constant temperature water bath at the appropriate temperature. $\dot{V}O_2$ was measured as the ml of O_2 injected into the respiration vessel necessary to level the manometer fluid. All measurements were taken at night in the dark under approximately standard conditions (post-absorptive, resting in the dark, during their minimal daily activity; Bennett and Dawson 1976).

Respiration chambers were sealed, placed in the water bath at 1800 h CST, and O_2 added as needed to maintain equal pressure in both chambers. Hourly measurements were taken

from 2400 to 0600 h. This regime allowed turtles, chambers and waterbath to become thermally equilibrated and turtles to become quiescent. $\dot{V}O_2$ of each turtle was measured first at the AT for two nights, then on successive nights, $\dot{V}O_2$ was measured acutely at 10, 15, 20, 25, 30, and 35°C. Acute $\dot{V}O_2$ measurements at temperatures higher than AT were alternated with measurements at temperatures lower than AT, as much as possible, to prevent turtles becoming acclimated to temperatures higher or lower than AT over the course of the measurements.

Measurements taken the first night were consistently higher and more erratic than the second night and were excluded from analyses. The lowest consecutive three hourly measurements between 2400 and 0600 h were averaged and converted to STP. The relation of $\dot{V}O_2$ to live body mass (LBM) was analyzed by least square linear regression, after log_{10} transformation of values. Energy equivalent of $\dot{V}O_2$ was 20.096 Kj/l O_2 (assuming turtles have a mixed diet, Brodie 1945). The body weight of turtles in $\dot{V}O_2$ trials was taken after each trial and, therefore, was an average of three to six measurements. The turtles were post-absorptive and had been in air (moist air inside respiration chambers) approximately 10 h before weights were taken.

The daily field metabolic rate (FMR), including increased metabolism due to activity, was estimated by

multiplying resting metabolic rates at the appropriate
temperature by 1.5 for the days turtles were active. Because
field metabolic rate data are not available for turtles,
this value (1.5) was derived from data for lizards. A
comparison of resting metabolic rates in lizards at $30^{\circ}C$
(Bennett and Dawson 1976) and field metabolic rates in
iguanid lizards during their active season (Nagy 1982),
corrected to 24 h for a 1000 g animal, produced a value of
approximately 1.5.

Age-specific annual metabolic heat loss was calculated
by the formula

$$R = \sum_{t=10}^{30} (a_t * LBM^{bt}) * 24\ h * D_t * C_t \qquad (3)$$

where t = temperature regime (10, 15, 20, 25, $n0^{\circ}C$)

a and b = intercept and slope, respectively, of

temperature-specific VO_2-body mass regression

equation

LBM = live body mass in g, average for age class

D = days included in temperature regime

C = an adjustment factor to include activity;

equals

(proportion of temperature regime turtles are

active* 1.5) + (proportion of temperature

regime turtles are inactive * 1)

Production

Production, elaboration of new biomass, can be divided

into growth, reproduction, storage, exuvia and secretions. Exuvia and secretions are considered to constitute a relatively minor portion of the turtle's energy budget and were ignored.

Turtles were trapped at several areas around Moss Lake between February and October 1977, returned to the lab and frozen within 3 days. The date turtles were frozen was considered a sample date. Turtles were weighed, measured, then dissected. Individuals were compartmentalized into carcass (including viscera), shell, dissectable fat and reproductive tissue. Dissectable fat included large pads of fat near the skin of the leg insertions and smaller bodies of fat in mesenteries throughout the body cavity that could be removed by gross dissection. Removing as much fat as possible by dissection facilitated drying and homogenizing body tissues. Carcass and shell were dried at 60°C, and dissectable fat was dried at 40°C and -15 psi to constant weight. Testes were weighed and preserved in 10 per cent formalin. Ovarian follicles and oviducal eggs were counted, measured, and weighed, and corpora lutea were counted. Oviducts, oviducal eggs, ovaries and, in some cases, ovarian follicles 10-20 mm and greater than 20 mm in diameter, were dried separately at 40°C and -15 psi.

Dried tissue was ground and homogenized either in a Wylie Mill[tm] or by mortar and pestle. Aliquant samples were used to determine ash, lipid and energy content of selected

samples. Ash content was determined by burning 1-2 g samples in a muffle furnace at $600^{\circ}C$ for at least 6 h. Lipid content was determined by chloroform : methanol (2:1) extraction. Approximately 5 g aliquants of selected tissues were dried at $40^{\circ}C$ and -15 psi, weighed into a flask, covered with solvent (1 g tissue to 20 ml solvent) and heated to $40^{\circ}C$ for 24 h with constant agitation. Tissue samples were then filtered through tared, dried filter paper discs and washed with solvent. Disc and lipid-free tissue were dried and weighed to determine lipid-free tissue weight. Energy content was determined by burning approximately 1 g aliquants of dried tissue in a Parr[tm] Adiabatic oxygen-bomb calorimeter.

Growth, increase in individual body mass, was estimated by first determining the individual dry mass (DM), dry lipid mass (DLM), and dry lipid-free mass (DLFM) of each somatic component (carcass, shell, and dissectable fat). DLM was determined by multiplying DM by the mean per cent lipid in aliquant samples of the given tissue, and DLFM was the difference between DM and the calculated DLM. DLM for each component were then summed for each individual to give an individual total dry lipid mass (TDLM). DLFM of dissectable fat was variable, but never accounted for more than 0.5 per cent of total DM and, consequently, was not considered in further analyses. Energy density was determined in a set of

aliquant samples of dry lipid-free carcass and shell and dry dissectable fat by calorimetry.

Linear regression analyses of $\log_{10}$ transformed carcass DLFM, shell DLFM, and TDLM on PL were performed for males and females. Predicted values from these analyses for given PLs were (1) summed to estimate total somatic mass and (2) multiplied by the appropriate energetic equivalent then summed to estimate total somatic energy content. The initial and final PL for each year class were predicted from equations relating PL to age, and total somatic mass and energy content were estimated for these PLs. The difference between initial and final somatic values in each year class was taken as age specific annual growth.

Reproductive effort was measured only in females as the biocontent of eggs. Energy devoted to courtship, production of sperm in males, movement related to locating mates and nesting areas, nest construction, and other activities relating to reproduction were not considered. Female age at sexual maturity, clutch frequency, clutch size, and oviducal egg size were estimated from the condition of the ovary and oviduct in dissected turtles. The estimate of energy devoted to growth and reproduction are net energy estimates and do not include the metabolic cost of producing the biomass.

Energy Budget

Each term in the energy budget equations,

$$C = A + (F + U) \qquad (4)$$

$$A = R + P \qquad (5)$$

$$P = Pg + Pr \qquad (6)$$

in which C = consumption, ingested as food,

A = net metabolizable energy,

F+U = feces and urine,

R = metabolic heat loss,

P = secondary production or new biomass,

Pg = somatic growth, and

Pr = reproductive tissues

was expressed as Kj y^{-1} and calculated for each year class for both sexes. Specific dynamic action (SDA) was not calculated directly, but was included in the metabolic heat production estimate. The energy content of nitrogenous waste was not determined. Consequently, A was actually net metabolizable energy. Reproductive effort (RE) was defined as the ratio of energy invested in eggs to net metabolizable energy (Pr/A).

R and P values were determined in Moss Lake P. scripta, then summed to estimate A. Since neither (F + U) or C were determined directly, these values were calculated using assimilation efficiency values (A/C) reported for other reptiles. Kepenis and McManus (1974) reported assimilation efficiencies of 79.7, 85.3, 84.3, and 88.8 per cent at 20, 25, 30 and 35°C, respectively, in juvenile Chrysemys picta

fed beef cardiac muscle. Nagy (1982) summarized the published data on metabolic efficiency

$$\frac{C - (F + U)}{C} \qquad (7)$$

in lizards, and reported values of about 55 per cent in herbivores and about 80 per cent in insectivores. Gut content examination indicated Moss Lake P. scripta feed primarily on aquatic vegetation and consequently have assililation efficiencies similar to herbivorous lizards of 60 per cent.

The life history energy budget was the sum of the individual annual budgets for all age classes through the maximum expected age:

$$A_{total} = \sum_{x=0}^{max} (R_x + Pg_x + Pr_x) \qquad (8)$$

Population Dynamics

The population size of P. scripta in the mark and release area (Figure 1) during 1978 was estimated by the Jolly stochastic multiple recapture method (Begon 1979). This model, as are almost all capture-recapture models, is based on the following assumptions: (1) all marks are permanent and are recognized correctly on recapture, (2) being captured and marked does not alter an individual's subsequent chance of surviving or being recaptured, and (3) all individuals, marked and unmarked, have an equal chance

of surviving and of being captured. In addition, the Jolly method assumes age-independent survival rate, although survival rate is not assumed to be constant through time.

The surface area of the mark and release area, entire lake, and area of water depth less than 5 m were determined from U.S. Geological Survey topographic maps (7.5 minute series; 1:24,000) with a compensating planimeter.

The PL of turtles captured for the first time in the mark and release area were tabulated by 1-mm increments by date and sex. The PLs at year intervals were calculated from equation 2 which relates PL to age, rounded to the nearest mm, and used to establish age classes. For example, all individuals with PL between that predicted for 1 y and 2 y were assumed to be 1 year old. The number in each age class, and the proportion of the total sample each age class accounts for, was then calculated. Multiplying those proportions by the estimated population density in the mark and release area was used to estimate the number in each age class (N_x) in the population. This technique assumes the age distribution in the sample represents the age distribution in the population.

The population energy budget was estimated for the mark and release area as the sum of the age specific individual energy budgets multiplied by the number of individuals in each age class, and expressed as Kj y^{-1} and Kj y ha $^{-1}$.

Age specific reproductive output (M_x) for females was determined from the PL-age equation 2 (which relates PL to age and was used to predict PL at the beginning of each year), the clutch size to PL estimate, and the clutch frequency estimate. The annual egg production of the population (N_o), was calculated as

$$N_o = \sum_{min=x}^{max} N_x \, M_x \qquad (9)$$

where N = number in the age class,

M = annual reproductive output, and

x = age class.

Survivorship schedules can be calculated in two basically distinct ways (Deevey 1947). A horizontal life table follows a cohort of animals from birth until the last member dies. Survivorship is calculated by dividing the number surviving to age x by the original cohort size. A vertical life table is based on the distribution among age classes during a short period of time, where survivorship is calculated by dividing the number in each age class by the number in the youngest age class. Vertical life tables are based on the assumption that the population has a stable age distribution and produces a hypothetical cohort that has existed its entire life under environmental conditions similar to the period of sampling. Vertical life tables are

most applicable in short term studies of turtles which may
live 30 y or more.

Estimated annual egg production was taken as the
initial cohort (N_o) and divided into each age class (N_x) to
produce a survivorship schedule (l_x). This technique
includes mortality suffered by the eggs in the nests as well
as mortality related to the aquatic environment.

CHAPTER V

RESULTS

Age Determination

The relation of growth rate (GR) to mean plastron
length (MPL) with 95 per cent confidence intervals for the
mean and for individual predicted values (SAS Institute Inc.
1982) is shown in Figures 2 and 3 for males and females
respectively. GR is significantly related to MPL in both
sexes (P<0.001) though MPL accounts for only 29 per cent of
the variation in GR in males and 48 per cent in females.

Solving for the integration constant, c, in equation 2,
requires a measure of turtle size at some known age.
Pseudemys scripta usually hatch at 90 days with a PL of
approximately 30 mm (Cagle 1950, Webb 1961, this study).
Consequently, 30 mm PL at an age of 90 days was taken as a
known size-age relation for males and females. Variance in
the growth curve relating PL to age was estimated as
follows: (1) the upper and lower 95 per cent confidence
limits for both the mean and individual predicted values
were treated as straight lines, parallel to the regression
line; (2) a Y-intercept value (a) was estimated for each
line by estimating its vertical distance from the regression

Figure 2. Relation of growth rate to mean plastron
length in male Pseudemys scripta. Inner narrow
lines indicate 95 per cent confidence interval
for the mean. Outer narrow lines indicate 95
per cent confidence interval for individual
predicted values.

Figure 2

Figure 2

$Y = 0.0876 + (-0.00039)$ PL

$R^2 = 0.29$

$N = 166$

MEAN PLASTRON LENGTH (mm)

GROWTH RATE (mm PL.d^{-1})
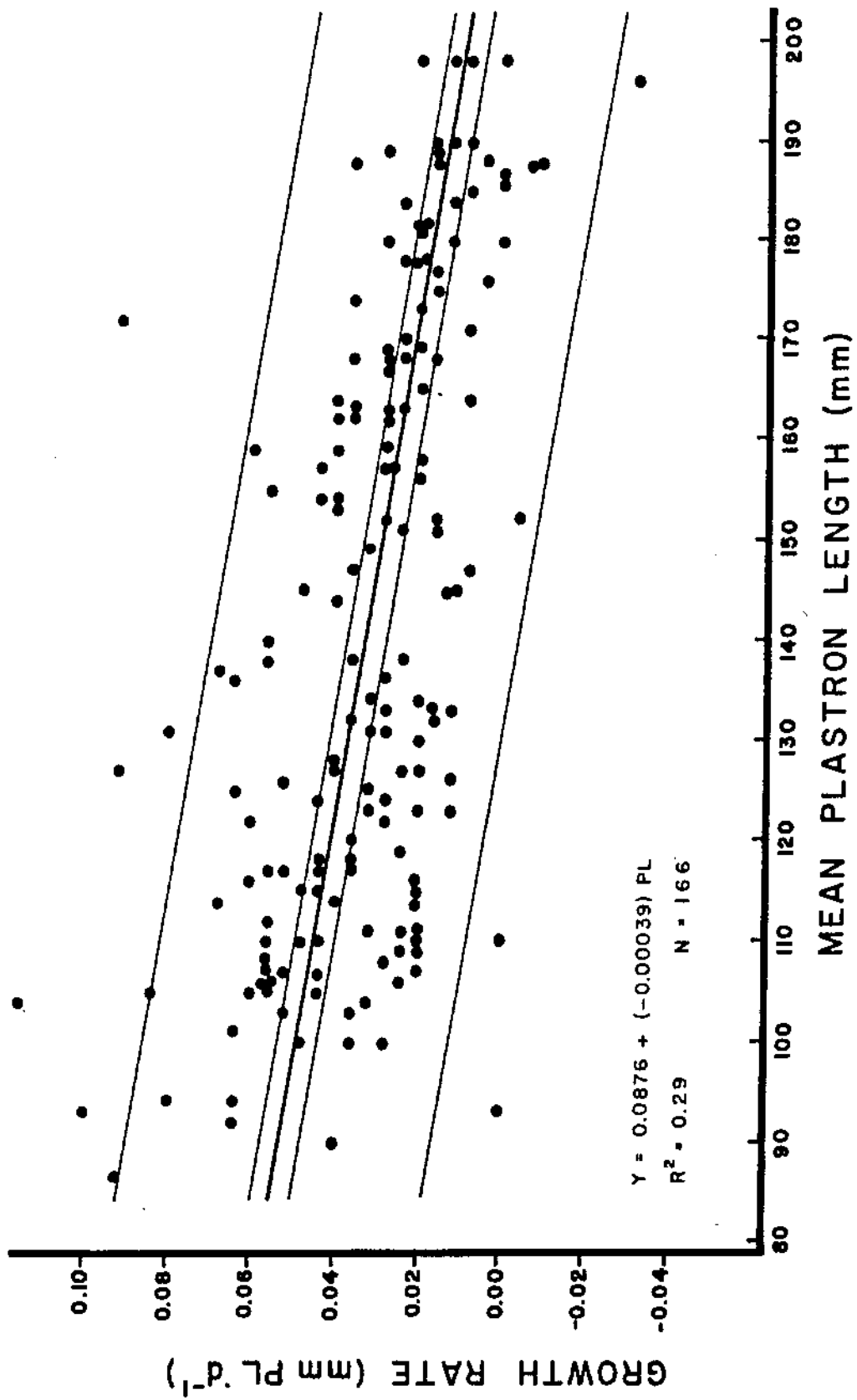
Figure 3. Relation of growth rate to mean plastron
length in female _Pseudemys_ _scripta_. Narrow
lines same as in Fig. 2.

Figure 3

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Figure 3

line; (3) the equation for each line was treated as a differential equation and intergrated, as was the regression line, to produce an equation relating PL to age; (4) 30 mm PL at 90 days was taken as a known age-size relation in the calculation of the integration constant, c, for all lines. The resulting set of growth curves relating PL to age and approximate 95 per cent confidence limits are shown in Figures 4 and 5 for males and females, respectively.

PL at yearly intervals was estimated by substituting values of PL in the growth equations so that age equaled multiples of 181 days. Age is calculated in days and only days during the 181-day active period (1 April through 30 September in Moss Lake, see comments below) are counted because growth is insignificant during the remainder of the year. Therefore, age in days divided by 181 equals age in years. Predicted age-PL and age-live body mass (LBM) relations are listed in Tables I and II for males and females, respectively.

Metabolic Heat Loss

The relation between live body mass (LBM) and oxygen consumption ($\dot{V}O_2$) for males at acclimatization temperatures (AT) of 10, 15, 20, 25, and 30°C and for females at AT of 15, 20, and 25°C is given in Table III. Since only two females were measured at 10 and 30°C they were not included in the analysis. No consistent difference in $\dot{V}O_2$ was

Figure 4. Growth curve of male <u>Pseudemys</u> <u>scripta</u>.
Inner dashed lines indicate 95 per cent confi-
dence interval for the mean. Outer dashed
lines indicate 95 per cent confidence interval
for individual predicted values. This curve
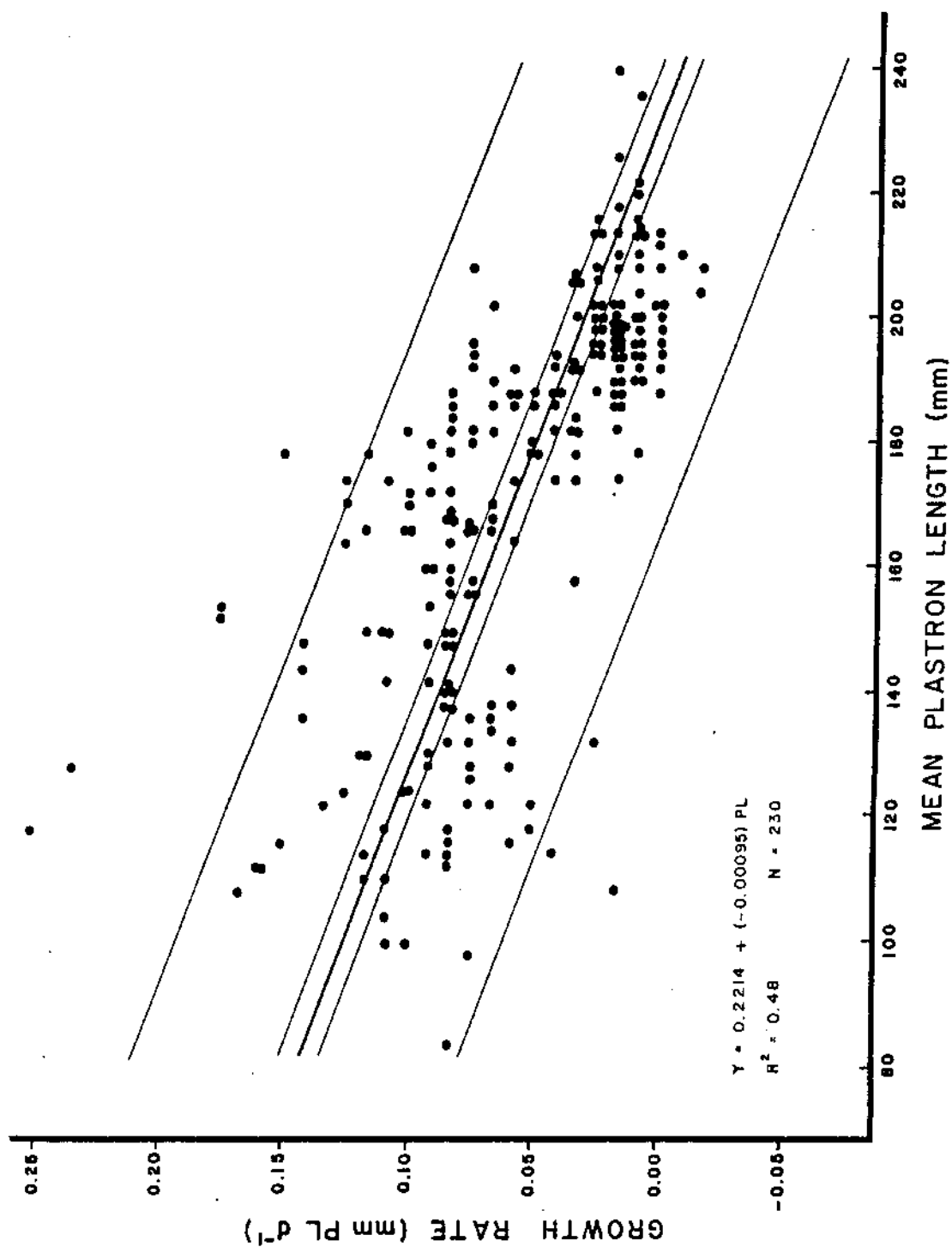is the integral form of the regression in Fig. 2.

Figure 4
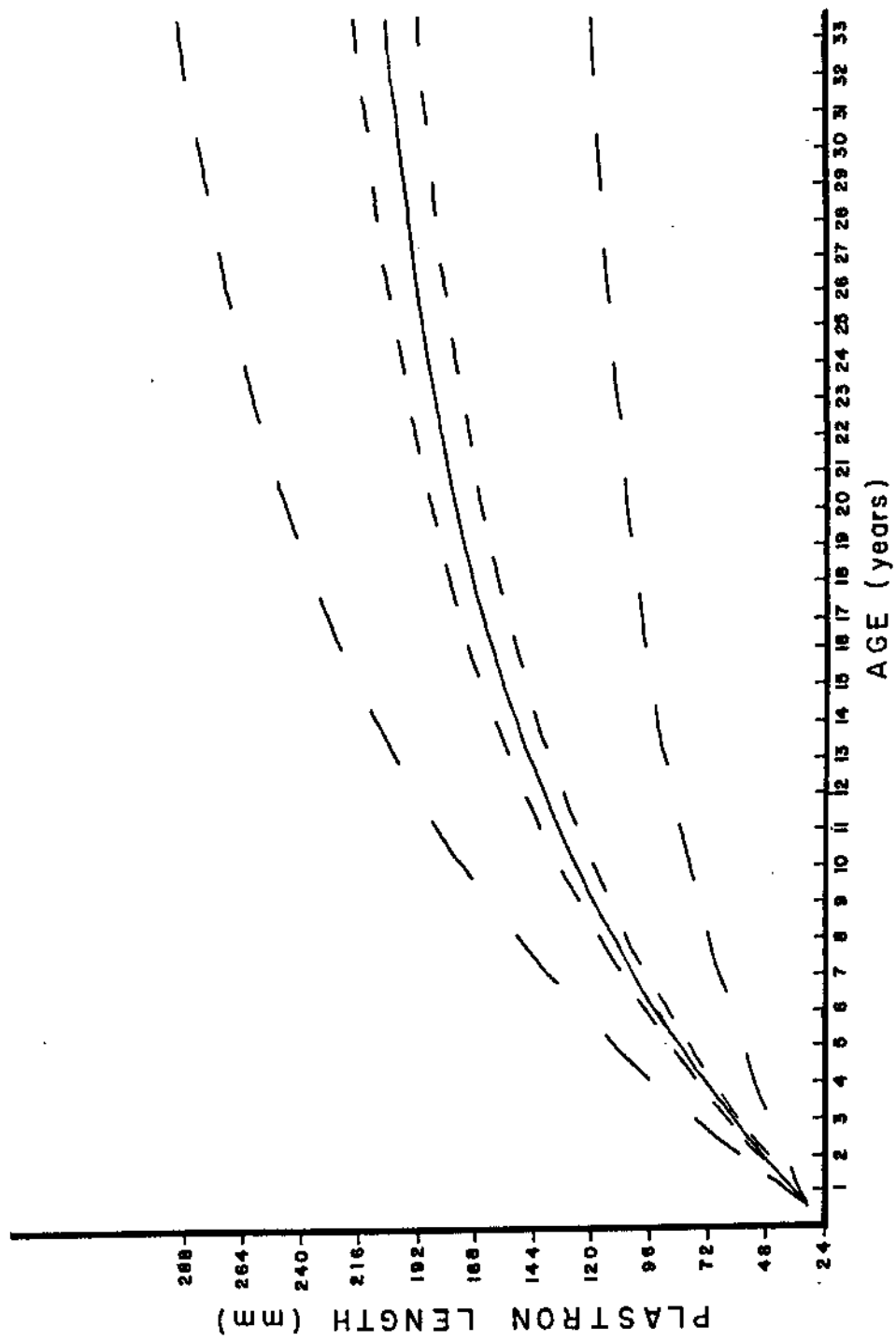
Figure 4

Figure 5. Growth curve of female _Pseudemys_ _scripta_.
Dashed lines same as in Fig. 4. This curve is
the integral form of the regression in Fig. 3.

Figure 5
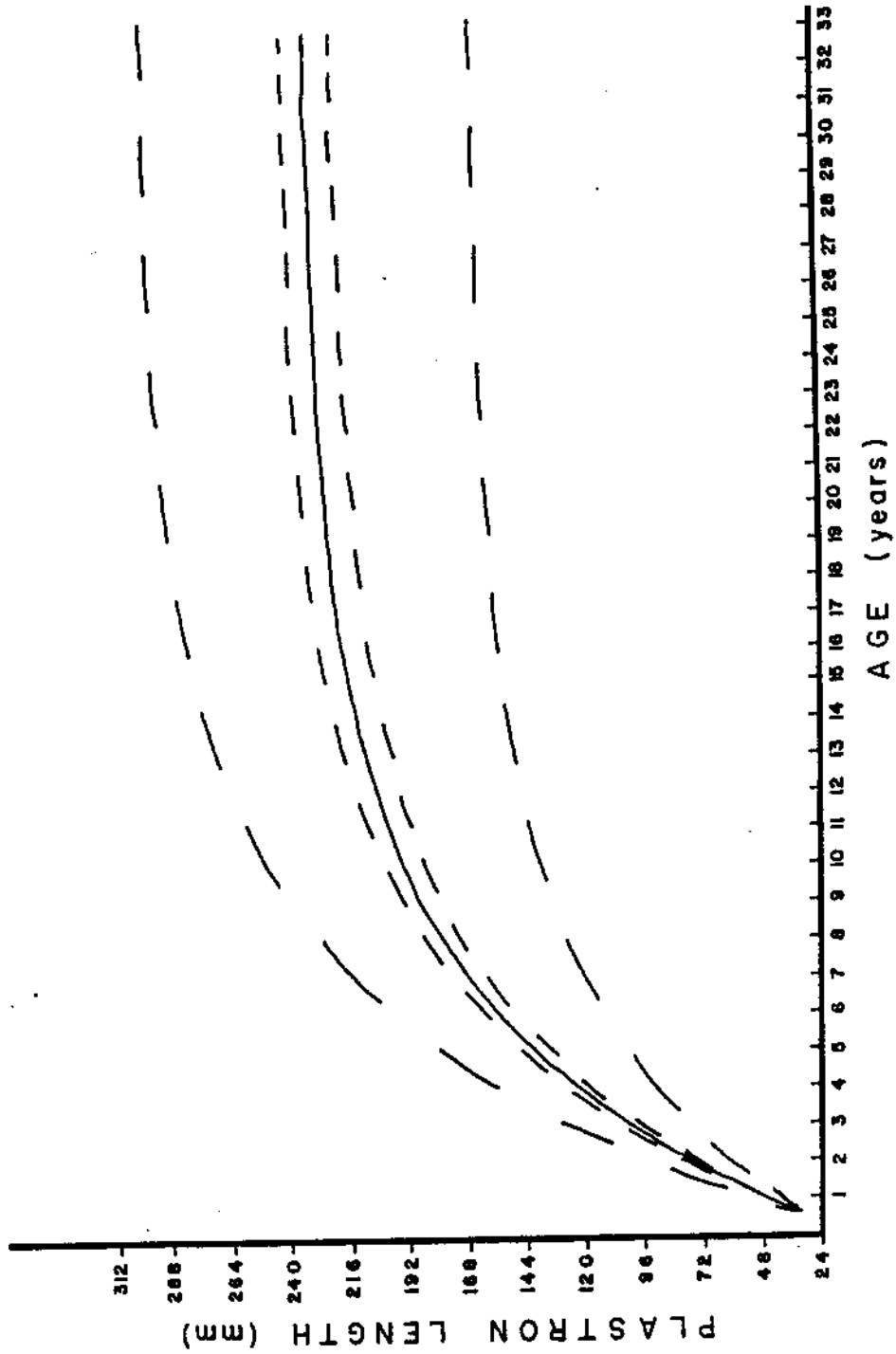
TABLE I

PREDICTED INITIAL AND AVERAGE SIZE OF ANNUAL AGE
CLASSES OF MALE Pseudemys scripta FROM MOSS LAKE

Age (y)	Initial* PL (mm)	Initial** LBM (g)	Average PL (mm)	Average LBM (g)
0.5	30	6	33	8
1	37	11	43	18
2	50	25	56	35
3	62	46	68	60
4	73	74	78	91
5	84	108	88	128
6	93	148	98	171
7	102	193	107	217
8	111	242	115	268
9	119	294	122	321
10	126	349	129	377
11	133	405	136	434
12	139	463	142	492
13	145	521	148	550
14	150	579	153	608
15	156	637	158	666
16	160	695	163	723
17	165	751	167	778
18	169	805	171	833
19	173	860	175	886
20	176	912	178	937
21	180	961	181	985
22	183	1010	184	1033
23	186	1056	187	1078
24	188	1100	190	1121
25	191	1143	196	1233

* PL = Plastron length.   ** LBM = Live body mass.

TABLE II

PREDICTED INITIAL AND AVERAGE SIZE OF ANNUAL AGE
CLASSES OF FEMALE Pseudemys scripta FROM MOSS LAKE

Age (y)	Initial PL (mm)[*]	Initial LBM (g)[**]	Average PL (mm)	Average LBM (g)
0.5	30	4	39	11
1	47	17	62	46
2	77	75	89	126
3	102	177	112	245
4	122	312	131	391
5	140	469	147	552
6	155	635	161	720
7	167	805	172	885
8	178	965	182	1042
9	186	1120	190	1189
10	194	1258	197	1321
11	200	1385	203	1441
12	205	1497	207	1547
13	210	1597	211	1640
14	213	1684	215	1721
15	216	1757	218	1790
16	219	1822	220	1850
17	221	1878	222	1902
18	223	1925	224	1946
19	224	1968	226	1985
20	226	2002	226	2017
21	227	2032	227	2044
22	228	2057	228	2066
23	228	2076	229	2086
24	229	2095	229	2102
25	230	2109	230	2133

[*] PL = Plastron length. [**] LBM = Live body mass.

detected between males and females. Because of considerable overlap among 95 per cent confidence belts (calculated for both sexes at 15, 20, and 25°C; Sokal and Rohlf 1969) and no significant differences among the slopes for the eight regression equations (P>0.75, test of equality of slopes, Sokal and Rohlf 1969), data for males and females were pooled at each temperature, and $\dot{V}O_2$-LBM relations were reanalyzed (Table III). A test of equality of slopes at all ATs again indicated the slopes were not significantly different (P>0.5). Thus, a common slope of 0.82, calculated within the test of equality of slopes, was used for the slope of a modified regression equation at each temperature. The y-intercepts (a) for the modified regression equations were calculated as follows for each AT:

$$\text{Log}_{10} \dot{V}O_2 = a + 0.82 \log_{10} \overline{\text{LBM}} \tag{10}$$

$$a = \log_{10} \dot{V}O_2 - 0.82 \log_{10} \overline{\text{LBM}} \tag{11}$$

where $\overline{\text{LBM}}$ is the mean live body mass in g and $\dot{V}O_2$ is the corresponding predicted $\dot{V}O_2$ in ml O_2 h^{-1} for the respective AT. The modified regression equations are listed in Table III.

Figure 6 is a plot of the annual lake temperature from February 1977 through December 1977. The number of days that

TABLE III

REGRESSION STATISTICS FOR O_2 CONSUMPTION $(\dot{V}O_2)^*$ on live body mass (LBM)** IN MOSS LAKE _Pseudemys_ _scripta_ OF FORM $\dot{V}O_2 = a\ LBM^b$

Sex	AT(^{O}C)***	N	a	b	r^2
M	10	11	.0348	.7531	.87
M	15	15	.409	.8155	.91
M	20	12	.0570	.8610	.95
M	25	13	.1849	.7898	.90
M	30	9	.0980	.9384	.64
F	10	2	---	---	---
F	15	5	.0363	.8131	.85
F	20	4	.0476	.8723	.995
F	25	4	.0760	.9557	.94
F	30	2	---	---	---
M+F	10	13	.0245	.8101	.89
M+F	15	20	.0506	.7749	.88
M+F	20	16	.0536	.8665	.95
M+F	25	17	.1508	.8275	.89
M+F	30	11	.0467	1.0436	.71
M+F	10****		.0230	.82	
M+F	15		.0384	.82	
M+F	20		.0715	.82	
M+F	25		.1579	.82	
M+F	30		.2067	.82	

*$\dot{V}O_2$ in ml O_2 h^{-1}.

**LBM in g.

***AT = Acclimatization temperature.

****Modified regression equations based on common slope.

Figure 6. Plot of annual temperature of Moss
     Reservoir. Water temperature was recorded
     continuously at 1 m at a location within the
     mark and recapture area. Circles represent
     the mean hourly water temperature for one
     week intervals.

Figure 6
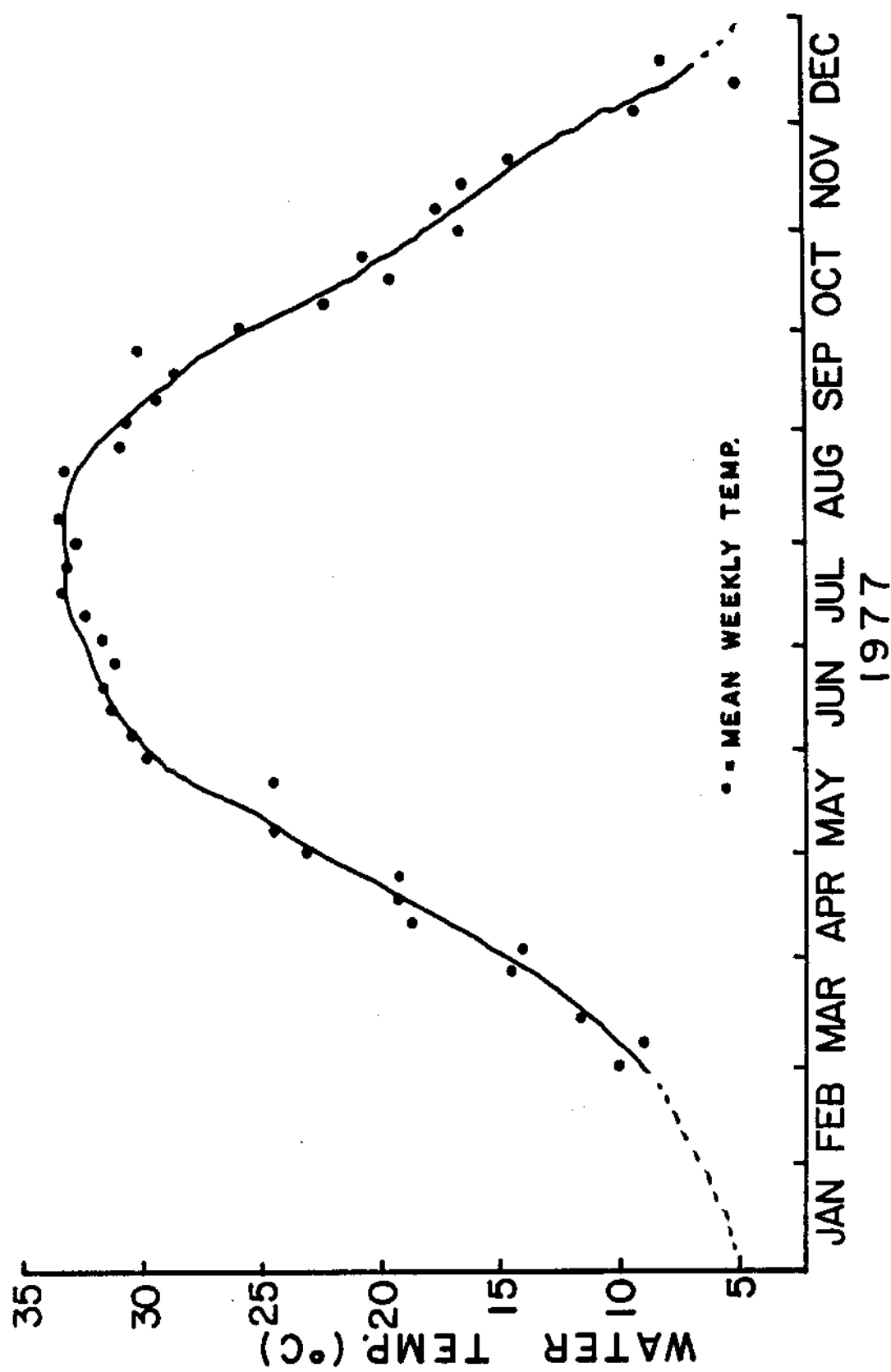
water temperature centered around the five ATs was estimated as 115 days at 10°C (below 12.5°C), 49 days at 15°C (12.5-17.5°C), 41 days at 20°C (17.5-22.5°C), 35 days at 25°C (22.5-27.5°C), and 125 days at 30°C (above 27.5°C). Annual metabolic heat loss was estimated by assuming that turtle body temperature was equal to water temperature (i.e., 10° for 115 days, 15° for 49 days, 20° for 41 days, 25° for 35 days, and 30° for 125 days).

Turtles were assumed to be inactive when water temperature was below 20°C (184 days, October-March), based on the following observations: (1) mark and recapture data indicated very little growth for most turtles; (2) very few turtles were trapped; (3) turtles that were trapped generally had empty digestive tracts; and (4) aerial basking was infrequent.

Age specific annual metabolic heat loss (R_x) for male and female Moss Lake P. scripta (Table IV) was estimated based on the following assumptions: (1) during the days when turtles were active, their metabolic rate was 1.5 times standard laboratory rates at appropriate temperatures; (2) during the 20° regime (17.5-22.5°), the water temperature is assumed to be below 20° for half of the 41 days during which turtles are inactive; (3) active days include a period of 181 days (April-September); and (4) during the 184 inactive

TABLE IV

AGE SPECIFIC ANNUAL AND TOTAL LIFE HISTORY FIELD METABOLIC
HEAT LOSS (R) IN MOSS LAKE Pseudemys scripta

Age (y)	Male $\dot{V}O_2$ (l)	Male Energy Equivalent (Kj)[*]	Female $\dot{V}O_2$ (l)	Female Energy Equivalent (Kj)[*]
0.5	7	149	9	187
1	14	281	31	619
2	25	497	70	1408
3	38	764	120	2421
4	54	1076	177	3554
5	71	1425	235	4722
6	90	1802	292	5869
7	109	2197	346	6950
8	130	2609	396	7949
9	151	3030	441	8855
10	172	3453	480	9656
11	193	3875	516	10366
12	214	4293	547	10988
13	234	4707	574	11530
14	254	5111	597	11990
15	274	5506	616	12382
16	293	5889	633	12725
17	311	6255	648	13016
18	329	6611	660	13265
19	346	6956	671	13481
20	362	7281	680	13660
21	378	7591	687	13811
22	393	7889	693	13933
23	407	8172	699	14039
24	420	8441	703	14131
25	454	9124	712	14301
Total	5723	114984	12233	245808

[*] 20.096 Kj l^{-1} O_2.

days, field metabolic rates equal standard laboratory rates at the appropriate temperature.

The LBM to PL relation was calculated from weights and PLs of turtles used in $\dot{V}O_2$ trials. Fluids in the urinary bladder and cloacal bursa, food in the digestive tract, and water on the surface, increase the variation in LBM. The manner in which turtles were maintained during $\dot{V}O_2$ trials, and the averaging of individual turtle weights from three to six measurements, reduced the effect of these variables. Turtles were post-absorptive, thereby eliminating variation due to food in the digestive tract. Also, turtles had been in air (moist air inside respiration chambers) approximately 12 h preceding weight measurements, allowing most surface moisture and presumably much of the water in the urinary bladder and cloacal bursa to be lost. LBM was related to PL by the equations:

$$Log_{10}\ LBM = -3.8504 + 3.0388\ log_{10}PL \tag{12}$$

or

$$LBM = 0.000141\ PL^{3.0388} \tag{13}$$
$$(N=26,\ r^2=0.986)$$

in females and

$$Log_{10}\ LBM = -3.4513 + 2.8542\ log_{10}PL \tag{14}$$

or

$$LBM = 0.000354 \ PL^{2.8542}$$

(15)

$$(N=65, \ r^2=0.983)$$

in males. From these equations, the mean annual LBM was calculated from the mean annual PL.

Production

Values for component dry mass (DM), dry lipid mass (DLM), dry lipid-free mass (DLFM), and totals were determined. The relations of carcass DLFM, shell DLFM and total dry lipid mass (TDLM) to PL in males and females are shown in Figures 7 through 12, respectively. Energy density values are given in Table V. Gross energy density values (ash included) were used to estimate size specific energy content because ash mass was included in size specific mass estimates. Age specific annual growth in mass and energy content (Pg_x), for both sexes, are given in Table VI.

Figure 13 shows how ovary and oviduct condition was used to determine reproductive maturity, clutch frequency, and clutch size. Females with oviducal eggs, corpora lutea, or yolked ovarian follicles greater than 20-25 mm were judged to be sexually mature. The smallest mature female was 185 mm PL, collected 10 June. A 186-mm PL female marked and released in late June had oviducal eggs detected by palpating the posterior limb insertions. Only one (193 mm PL) of ten dissected females greater than 190 mm PL from May

Figure 7. Relation of carcass dry lipid-free mass
(DLFM) to plastron length in male <u>Pseudemys</u>
<u>scripta</u>.

Figure 7

Figure 7

$\log Y = 0.2905 + 0.0092 \; PL \qquad N = 22$

$R^2 = 0.93$

PLASTRON LENGTH (mm)
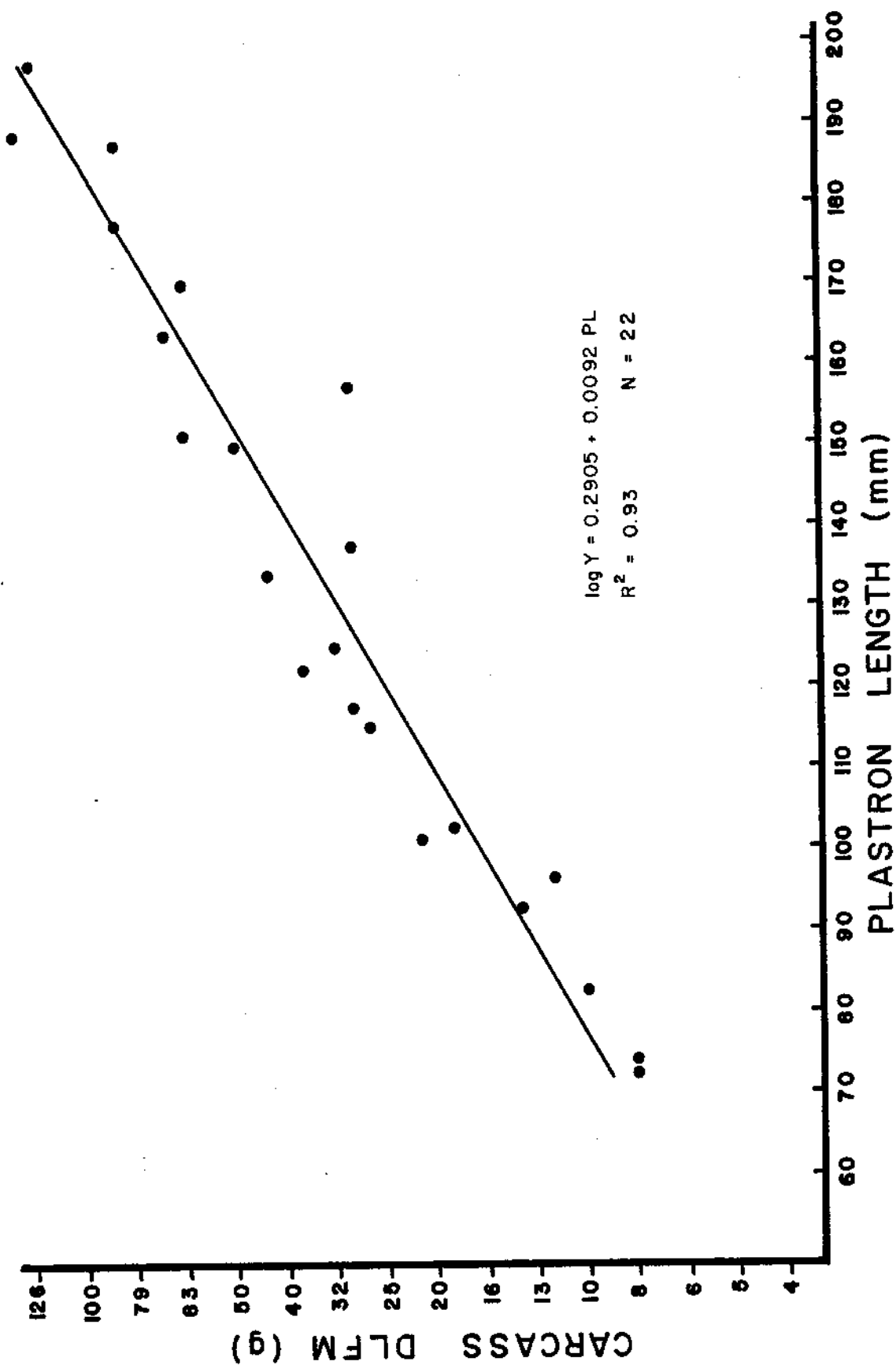
CARCASS DLFM (g)

Figure 8. Relation of shell dry lipid-free mass
(DLFM) to plastron length in male _Pseudemys_
scripta.

Figure 8

log Y = 0.3175 + 0.0115 PL   N = 18

R^2 = 0.97

PLASTRON LENGTH (mm)

SHELL DLFM (g)

51
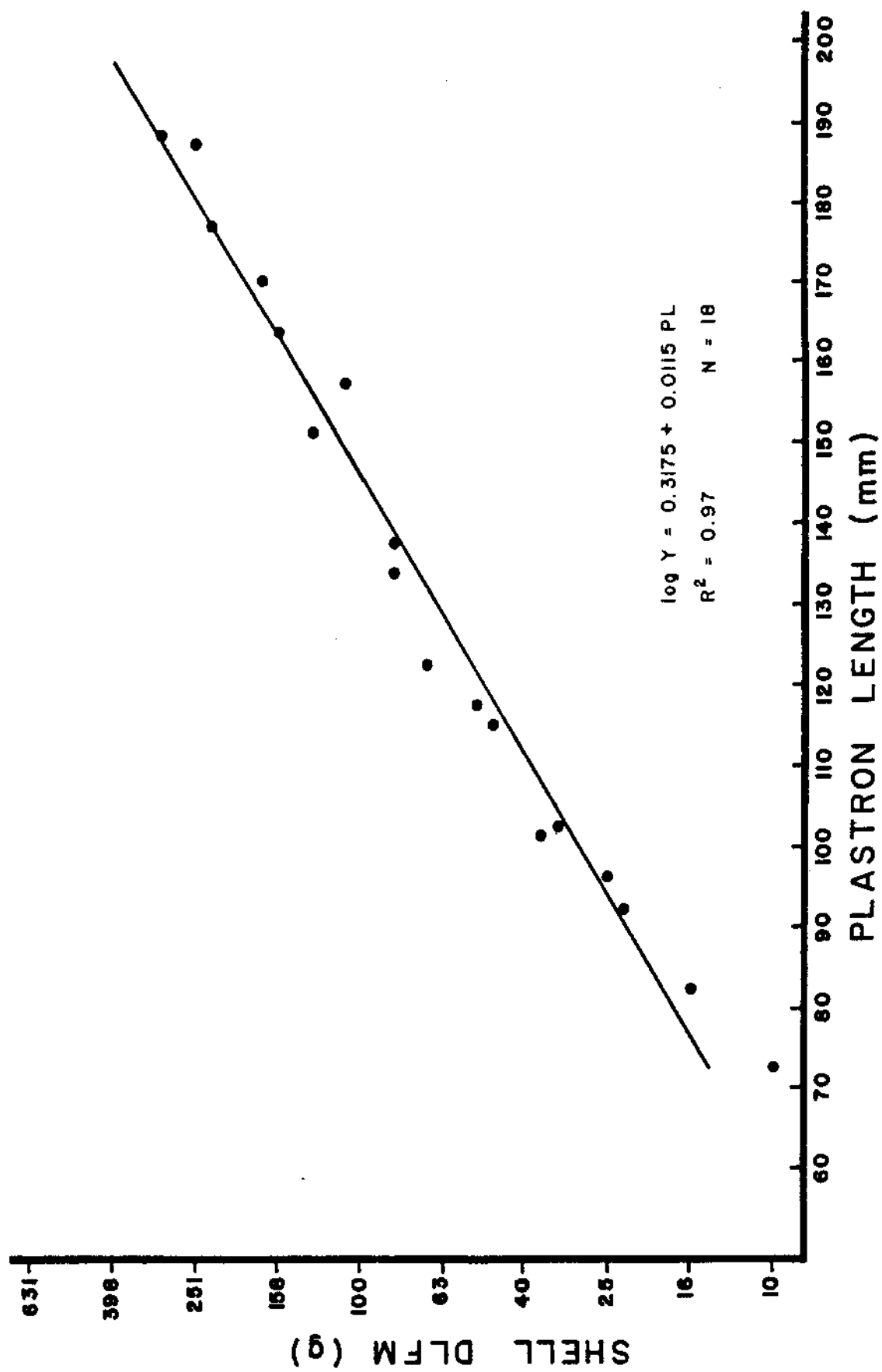
Figure 9. Relation of total dry lipid mass to
     plastron length in male <u>Pseudemys</u> <u>scripta</u>.

Figure 9

Figure 9

$\log Y = -0.685I + 0.0139 \; PL$ $N = 18$

$R^2 = 0.90$

PLASTRON LENGTH (mm)

TOTAL DRY LIPID MASS (g)
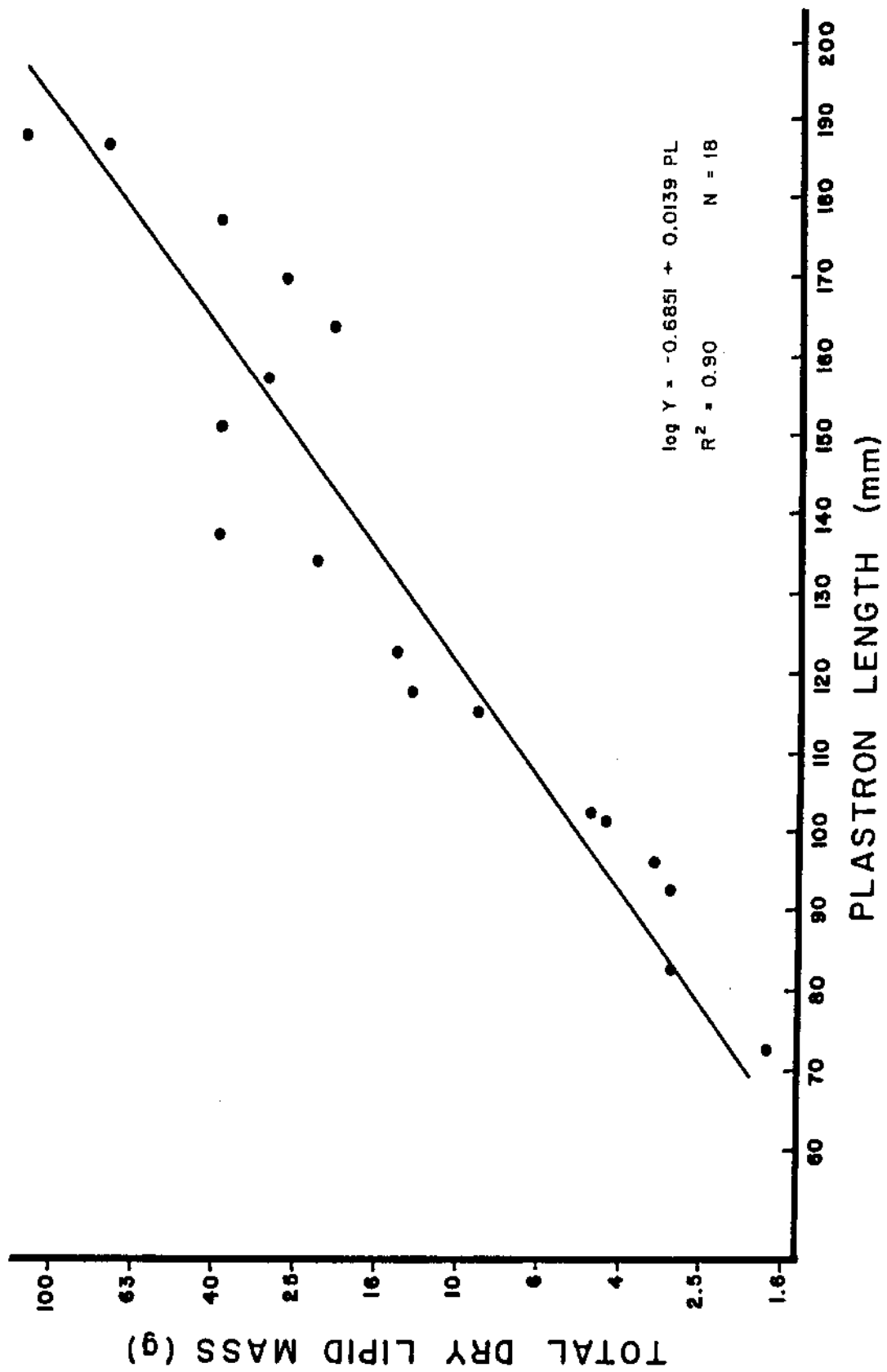
Figure 10. Relation of carcass dry lipid-free mass
     (DLFM) to plastron length in female <u>Pseudemys</u>
     <u>scripta</u>.

Figure 10

$\log Y = 0.3614 + 0.0081$ $N = 37$

$R^2 = 0.93$

PLASTRON LENGTH (mm)

CARCASS DLFM (g)
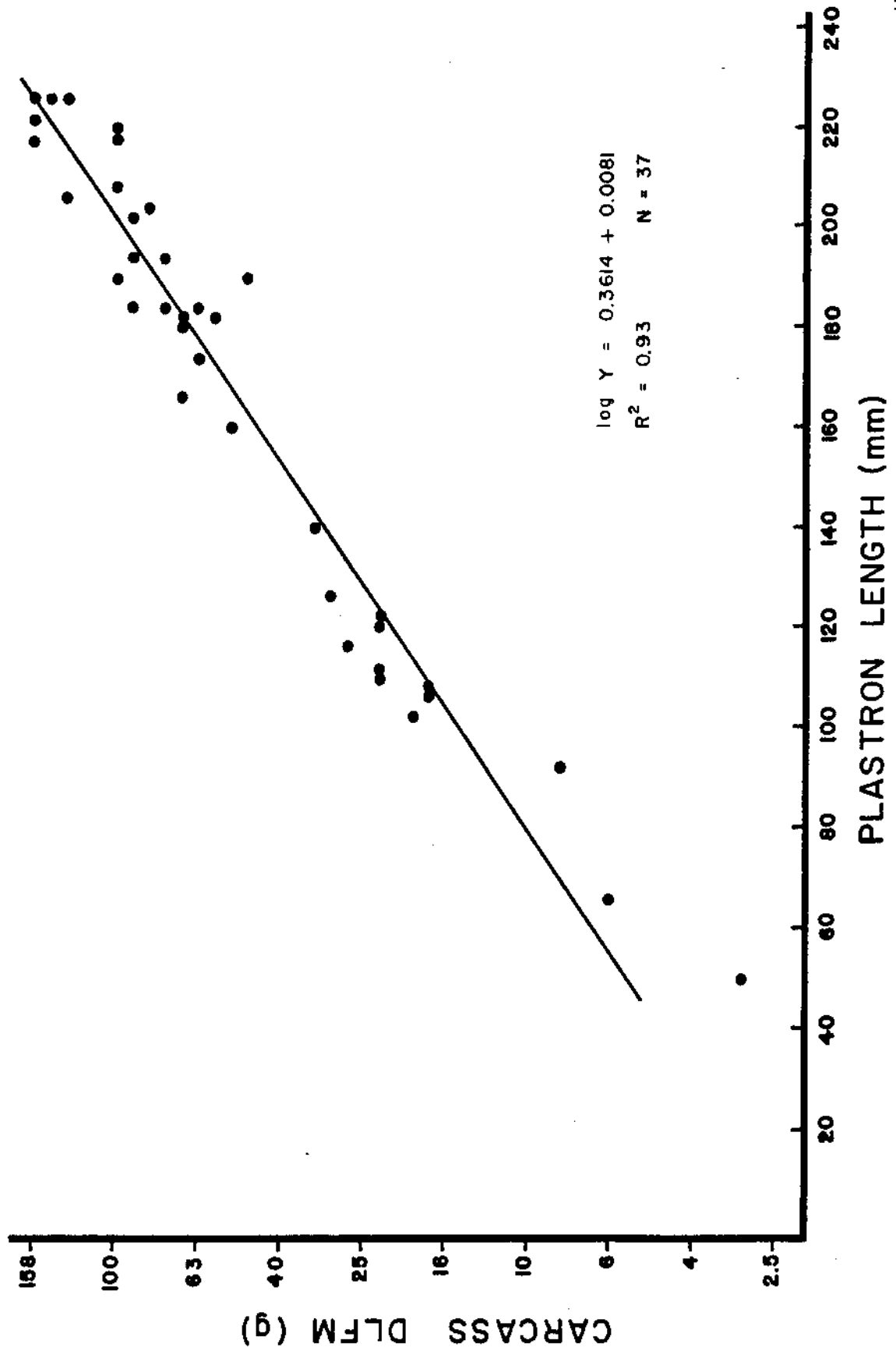
Figure 11. Relation of shell dry lipid-free mass
(DLFM) to plastron length in female Pseudemys
scripta.

Figure 11

log Y = 0.3116 + 0.0108 PL   N = 22

R² = 0.95

PLASTRON LENGTH (mm)

SHELL DLFM (g)
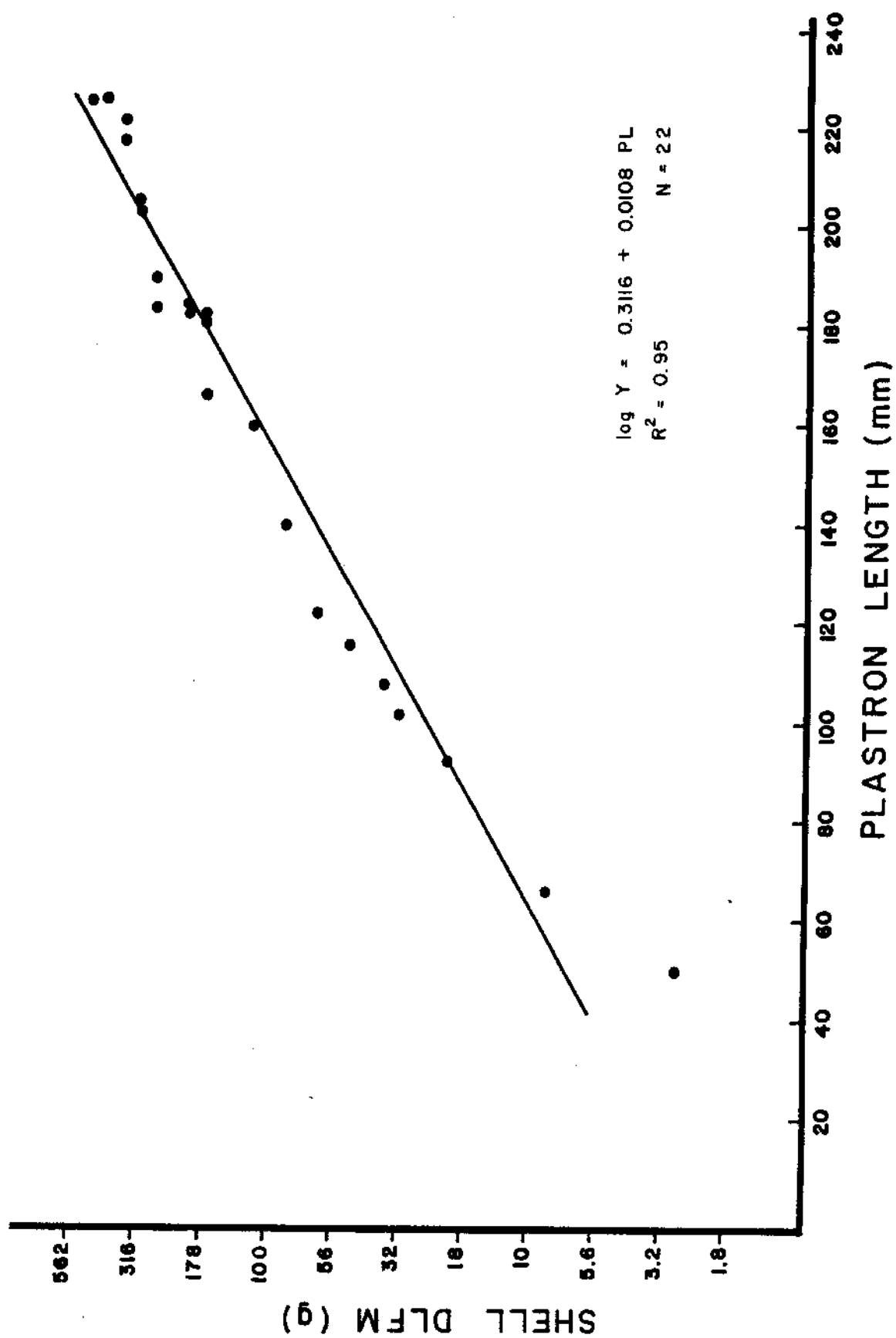
Figure 12. Relation of total dry lipid mass to
plastron length in female _Pseudemys_ _scripta_.

Figure 12

Figure 12

$\log Y = -0.8336 + 0.0137 \, PL$

$R^2 = 0.92$ $N = 22$

PLASTRON LENGTH (mm)

TOTAL DRY LIPID MASS (g)
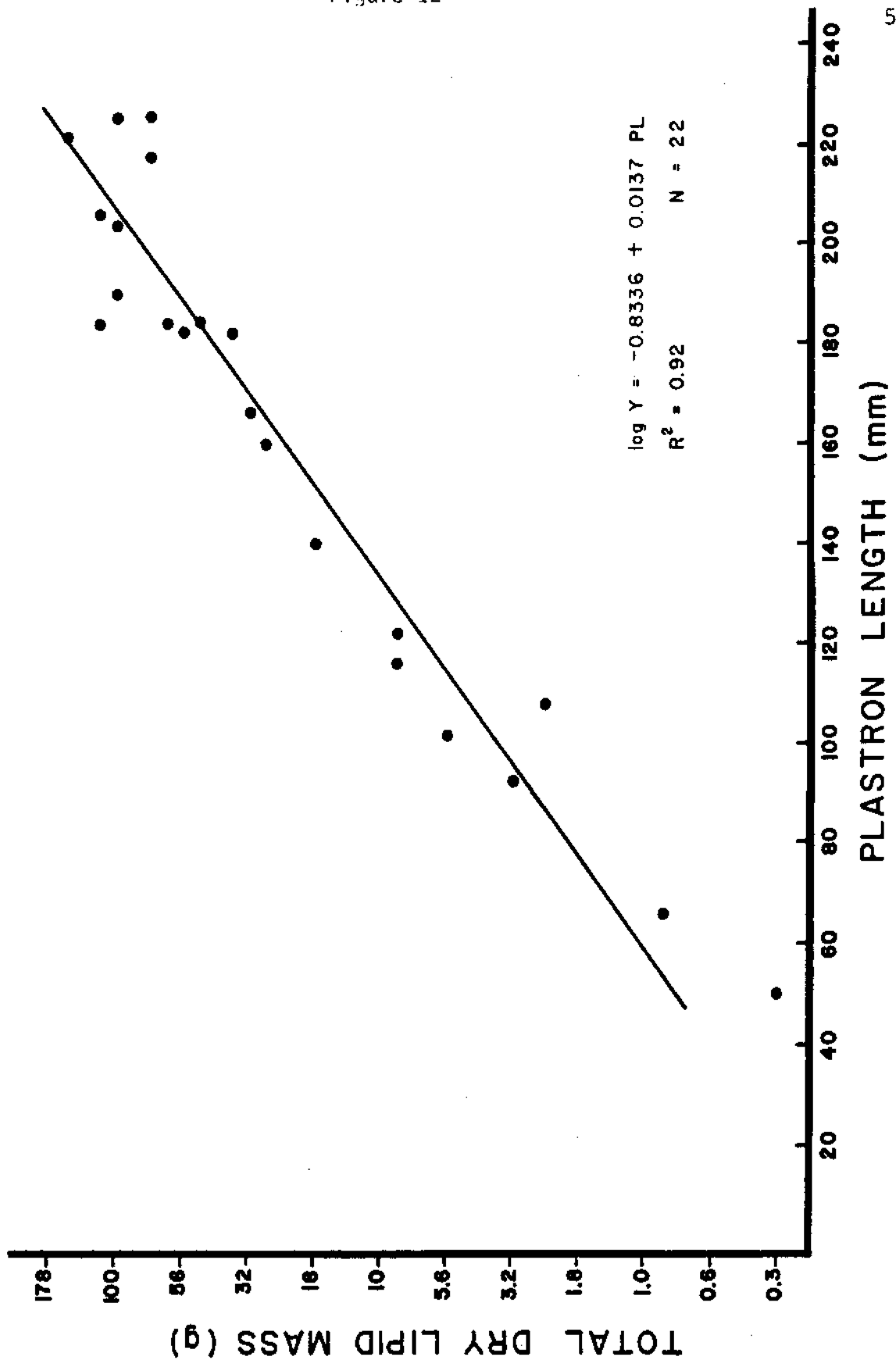
TABLE V

ENERGY DENSITY OF DRY TISSUE OF MOSS LAKE
Pseudemys _scripta_ EXPRESSED AS Kj g^{-1}

	N(n)[*]	Gross $\bar{X}$ ($\pm$ SD)[**]	Net $\bar{X}$ ($\pm$ SD)[***]
DLF Carcass	4(8)	18.22($\pm$0.50)	21.19($\pm$0.27)
DLF Shell	5(12)	8.64($\pm$1.33)	17.78($\pm$0.81)
Dissectable Fat	11(14)	37.61($\pm$0.78)	37.85($\pm$0.77)
Oviducal Eggs	9(35)	24.33($\pm$1.01)	26.52($\pm$0.60)

[*] N = Number of individual turtles and n = total number of samples.

[**] Gross = Ash included in sample.

[***] Net = Ash free sample.

TABLE VI

AGE SPECIFIC ANNUAL AND LIFE HISTORY GROWTH (P_g) IN MOSS LAKE Pseudemys scripta

Age (y)	Male Dry Mass (g)	Male Energy Content (Kj)	Female Dry Mass (g)	Female Energy Content (Kj)
0.5	1.6	24	4.1	58
1	3.9	57	12.2	174
2	5.0	73	19.5	280
3	6.3	92	27.9	409
4	7.6	113	37.5	560
5	9.3	138	46.4	706
6	10.9	163	55.1	855
7	12.7	191	60.3	950
8	14.8	223	66.2	1060
9	16.6	253	66.5	1080
10	18.6	285	67.0	1100
11	20.4	316	64.9	1078
12	22.5	349	62.1	1039
13	24.3	380	57.9	977
14	25.9	408	51.1	868
15	27.8	440	47.6	813
16	28.8	458	42.8	735
17	30.0	480	36.9	636
18	31.7	510	34.3	592
19	32.3	523	28.9	501
20	32.5	527	25.2	438
21	33.2	542	21.2	369
22	33.7	551	16.8	293
23	33.8	555	17.1	299
24	33.5	553	12.4	217
25	32.9	545	12.6	220
Total	550.6	8749	994.5	16307

Figure 13. Timing of reproductive events in female
    Pseudemys scripta. Adult females begin brumation
    with some yolked ovarian follicles 10-15 mm in
    diameter, less than one-seventh the volume of a
    follicle at ovulation the following spring.

Figure 13
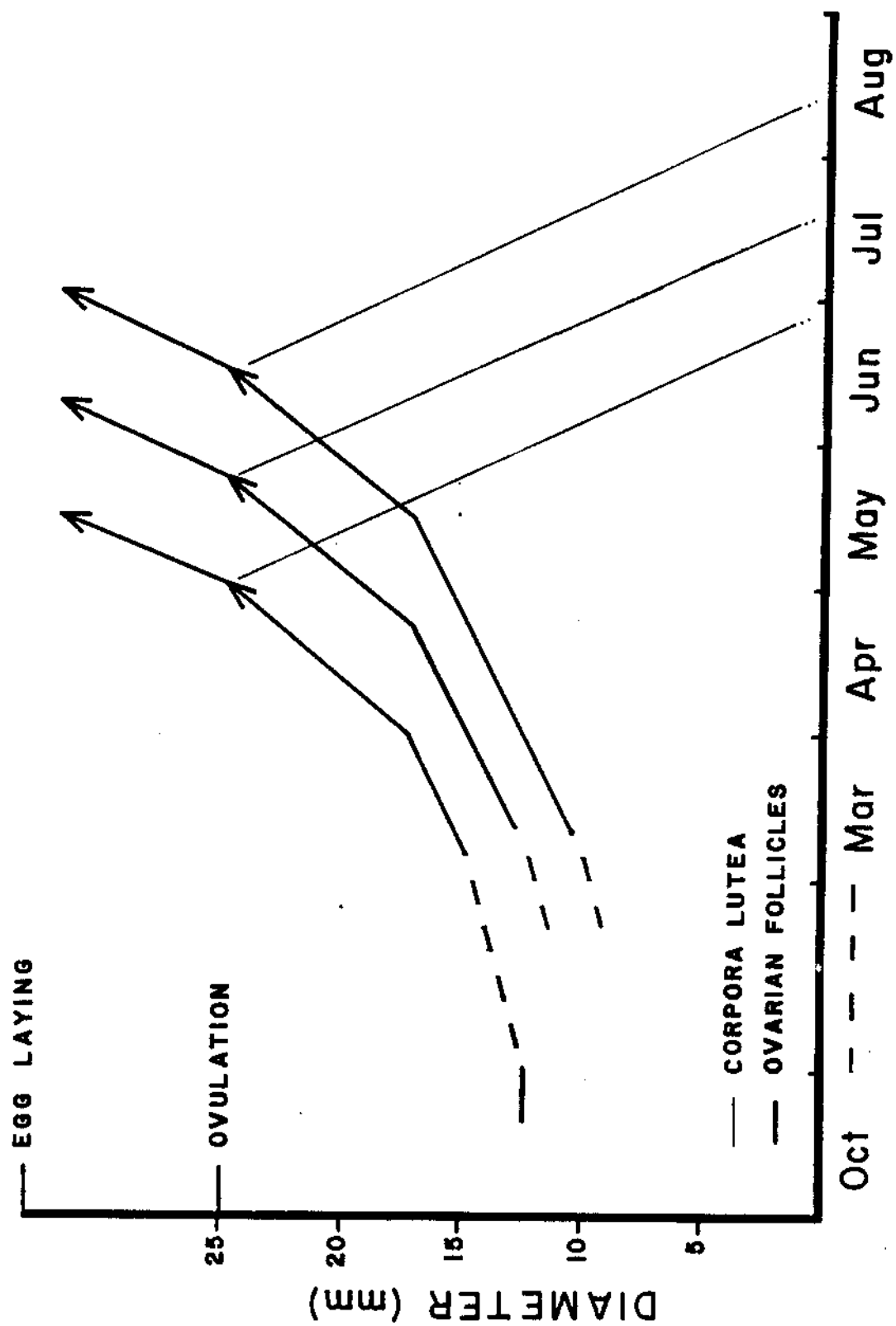
through June was not reproductively active. Females usually become sexually mature in their ninth year at 185-190 mm PL.

Large females (after one-two reproductive seasons) begin brumation with yolked follicles 10-15 mm in diameter. By late March, the largest follicles are 15-20 mm and are ovulated at 25 mm beginning in late April and early May. Egg laying occurs from mid-May through June. The latest oviducal eggs were observed, either by dissection or palpation, on 29 June. However, an absence of specimens from July precluded determining the fate of large ovarian follicles (15-20 mm) present in June. From late August through October no turtles had ovarian follicles greater than 15 mm.

Moss Lake *Pseudemys scripta* appear to have two or three clutches. The presence of two distinct sets of corpora lutea, and in some cases oviducal eggs (oviducal eggs corresponding in number to the most distinct set of corpora lutea), indicate that at least two clutches are produced by many individuals. The presence of large follicles (15-20 mm), in addition to oviducal eggs and corpora lutea, suggests that three clutches are possible. All dissected reproductively active females showed evidence that three clutches had been or would be produced, depending on the time during the reproductive season they were collected. For example, females from early May had greater complements of large (10-15 mm) yolked ovarian follicles and possibly

thinly shelled oviducal eggs. Females from June had distinct sets of corpora lutea and smaller complements of yolked follicles. The overlap in size of the larger follicles precluded recognizing distinct sets of follicles, and thereby estimating size and number of future clutches. In some individuals, sets of corpora lutea could be counted. In others, the smaller corpora lutea had deteriorated sufficiently to preclude an accurate count and were excluded from clutch size estimates. No corpora lutea were observed before May or after August, indicating that they do not persist from one breeding season to the next and, therefore, represent current reproductive activity.

Clutch size estimated from oviducal eggs was 7 to 14 (x=10.2; N=9). Clutch size estimated from distinct sets of corpora lutea, including those which corresponded to sets of oviducal eggs was 7 to 14 (x=10.3; N=20). Clutch size increased significantly with PL (Figure 14), as did mean dry egg mass within a clutch (Figure 15). Mean dry egg mass was obtained by dividing the total dry clutch mass by the number of eggs in that clutch.

The mean energy density of shelled oviducal eggs is given in Table V. The ratio of low energy shell to high energy yolk material, and therefore energy density, was assumed to remain constant with egg size. Analysis of

Figure 14. Relation of clutch size to plastron
length. Sets of corpora lutea which corresponded
to oviducal eggs were not included in analysis.

Figure 14
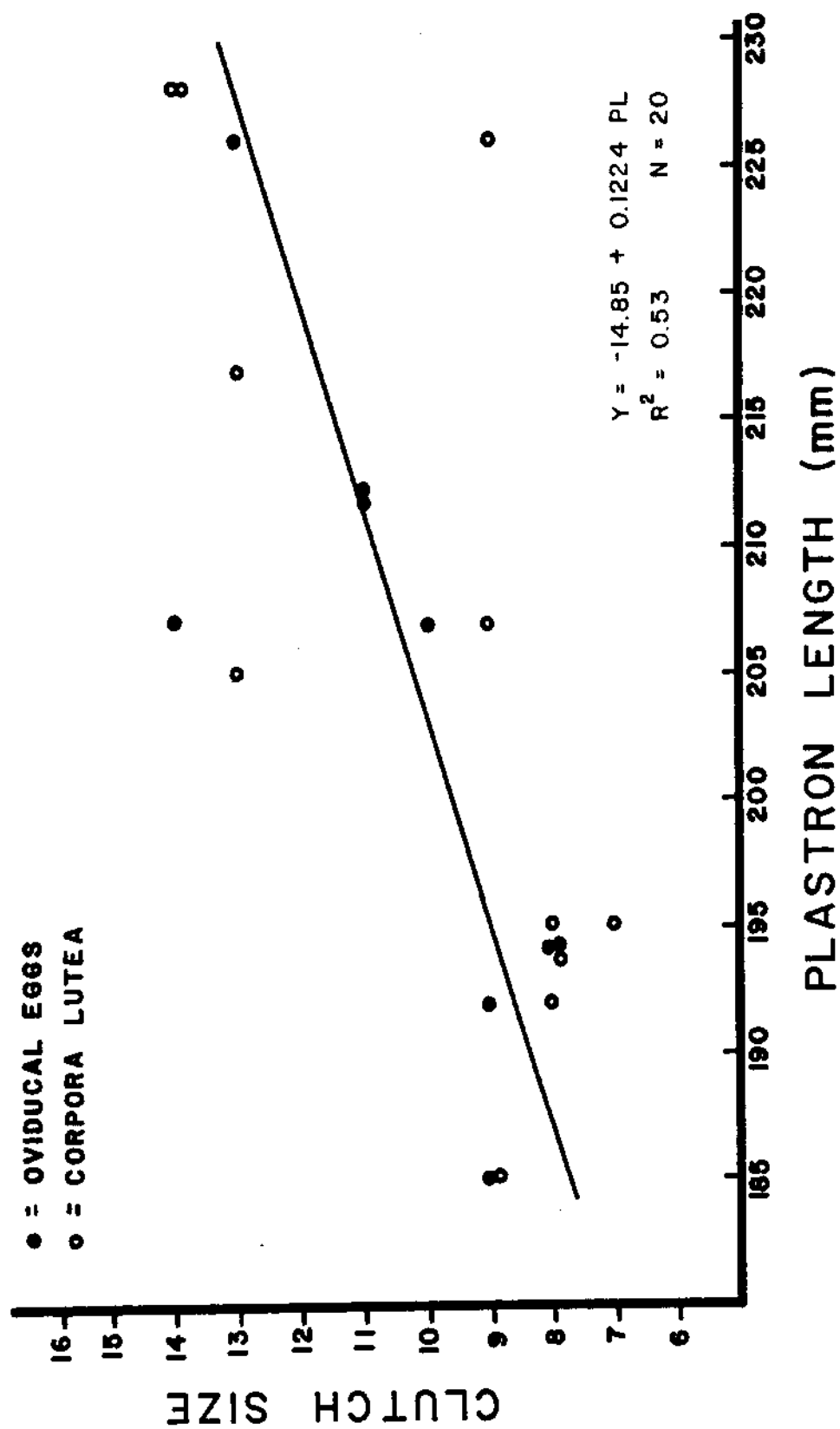
Figure 14

Figure 15. Relation of mean dry egg mass to plastron
length. The mean dry egg mass was obtained by
dividing the total dry clutch mass by the number
of eggs in that clutch.

Figure 15

Figure 15

$Y = -2.523 + 0.0262$ PL

$R^2 = 0.69$ $N = 9$

PLASTRON LENGTH (mm)
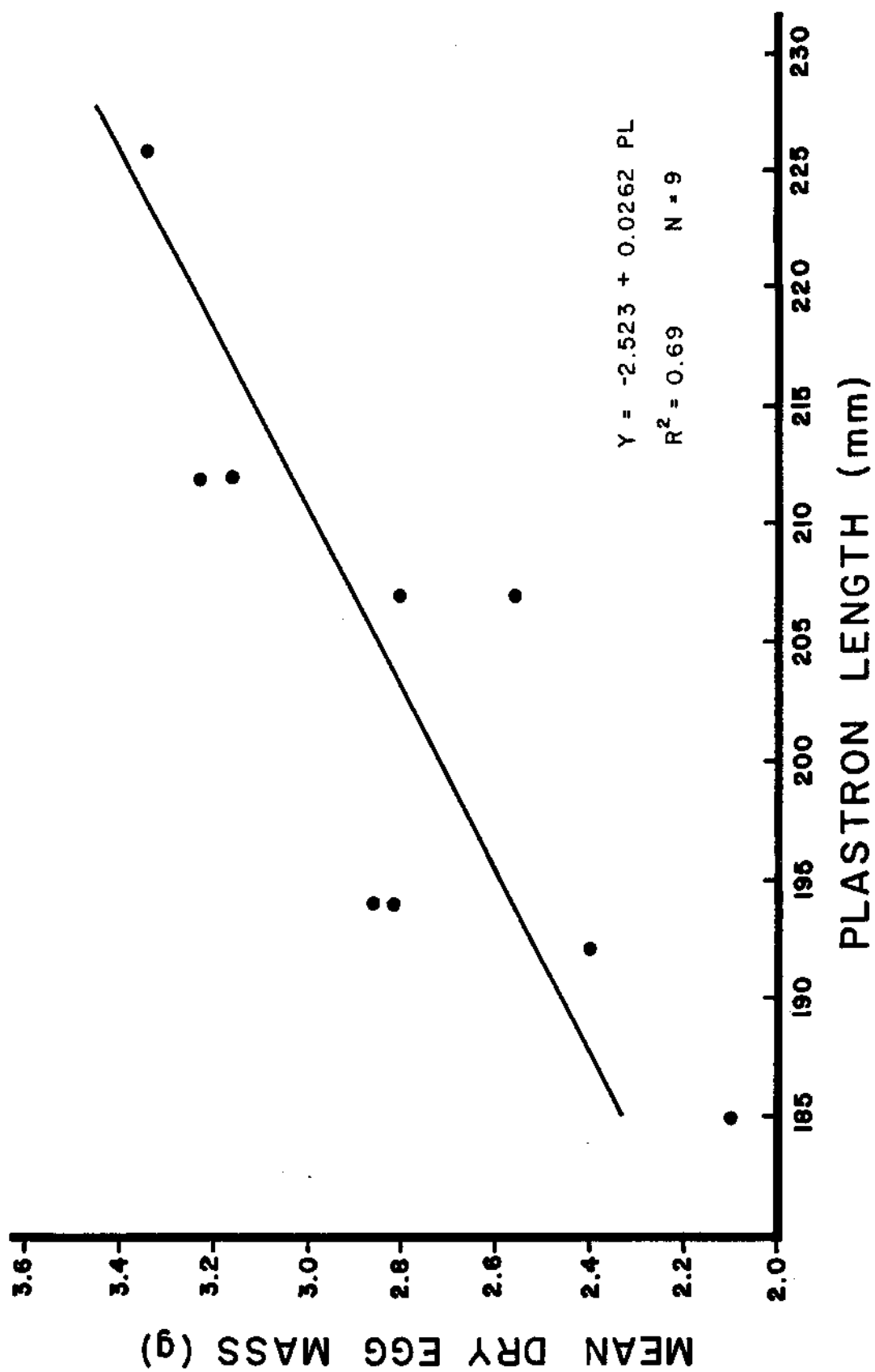
MEAN DRY EGG MASS (g)

variance showed that mean dry egg mass did not contribute significantly (P>0.25) to variation in energy density of ash-free eggs.

Age specific annual reproductive output (ARO) in dry mass (g) was calculated for females from the equation

$$ARO_x = (-2.523+0.0262 \ PL_x)*(-14.85+0.1224 \ PL_x)*3 \quad (16)$$

where PL_x was the predicted initial PL of age class x. The energy devoted to reproduction (Pr) was ARO * 26.523 jg^{-1}. Table VII shows age specific Pr in egg number, dry mass, and energy content.

Energy Budget

Annual and life history values for C, A, R, Pg and Pr and associated efficiencies are given for males and females, respectively, in Tables VIII and IX. The life history energy budget is the sum of age classes through 25 y, a life span near the maximum attained by Moss Lake _P. scripta._

Population Dynamics

Population size was calculated separately for males and females (N $\pm$ 2SE = 420 $\pm$ 142 and 411 $\pm$ 110, respectively) during 1978 within the mark and release area. The mark and release area includes a surface area of 8.2 ha, 5.2 ha of which has a water depth of less than 5 m. Population density for the mark and release area was approximately 51 males and

TABLE VII

AGE SPECIFIC ANNUAL AND LIFE HISTORY REPRODUCTIVE
OUTPUT (P_r) IN MOSS LAKE FEMALE Pseudemys scripta

Age (y)	Number of eggs	Dry Mass (g)	Energy Content(Kj)
0.5	0	0	0
1	0	0	0
2	0	0	0
3	0	0	0
4	0	0	0
5	0	0	0
6	0	0	0
7	0	0	0
8	0	0	0
9	24	56.4	1496
10	27	67.8	1799
11	29	78.3	2077
12	31	87.7	2324
13	32	96.0	2547
14	34	103.3	2741
15	35	109.4	2903
16	36	114.8	3047
17	37	119.5	3172
18	37	123.5	3276
19	38	127.0	3369
20	38	129.9	3446
21	39	132.4	3512
22	39	134.5	3567
23	39	136.1	3609
24	40	137.7	3652
25	40	138.9	3683
Total	595	1893.2	50222

TABLE VIII

AGE SPECIFIC AND LIFE HISTORY ENERGY BUDGET AND EFFICIENCIES FOR MALE MOSS LAKE Pseudemys scripta

Age	R	Pg	A*	C	R/A	P/A	P/R
0.5	149	24	173	288	.86	.14	.16
1	281	57	338	563	.83	.17	.20
2	497	73	570	950	.87	.13	.15
3	764	92	856	1427	.89	.11	.12
4	1076	113	1189	1982	.90	.10	.11
5	1425	138	1563	2605	.91	.09	.10
6	1802	163	1965	3275	.92	.08	.09
7	2197	191	2388	3980	.92	.08	.09
8	2609	223	2832	4720	.92	.08	.09
9	3030	253	3283	5472	.92	.08	.08
10	3453	285	3738	6230	.92	.08	.08
11	3875	316	4191	6985	.92	.08	.08
12	4293	349	4642	7737	.92	.08	.08
13	4707	380	5087	8478	.93	.07	.08
14	5111	408	5519	9198	.93	.07	.08
15	5506	440	5946	9910	.93	.07	.08
16	5889	458	6347	10578	.93	.07	.08
17	6255	480	6735	11225	.93	.07	.08
18	6611	510	7121	11868	.93	.07	.08
19	6956	523	7479	12465	.93	.07	.08
20	7281	527	7808	13013	.93	.07	.07
21	7591	542	8133	13555	.93	.07	.07
22	7889	551	8440	14067	.93	.07	.07
23	8172	555	8727	14545	.94	.06	.07
24	8441	553	8994	14990	.94	.06	.07
25	9124	545	9669	16115	.94	.06**	.07**
Total	114984	8749	123733	206222	.93**	.07**	.08**

*Net assimilated energy, Kj.

**Ratio of totals

TABLE IX

AGE SPECIFIC AND LIFE HISTORY ENERGY BUDGET AND EFFICIENCIES FOR FEMALE MOSS LAKE Pseudemys scripta

Age	R	Pg	Pr	P	A*	C	R/A	Pg/A	Pr/A	P/A	P/R	Pg/P	Pr/P
0.5	187	58	-	58	245	408	.76	.24	-	.24	.31	1	-
1	619	174	-	174	793	1322	.78	.22	-	.22	.28	1	-
2	1408	280	-	280	1688	2813	.83	.17	-	.17	.20	1	-
3	2421	409	-	409	2830	4717	.86	.14	-	.14	.17	1	-
4	3554	560	-	560	4114	6857	.86	.14	-	.14	.16	1	-
5	4722	706	-	706	5428	9047	.87	.13	-	.13	.15	1	-
6	5869	855	-	855	6724	11207	.87	.13	-	.13	.15	1	-
7	6950	950	-	950	7900	13167	.88	.12	-	.12	.14	1	-
8	7949	1060	-	1060	9009	15015	.88	.12	-	.12	.13	1	-
9	8855	1080	1496	2576	11431	19052	.77	.09	.13	.23	.29	.42	.58
10	9656	1100	1799	2899	12555	20925	.77	.09	.14	.23	.30	.38	.62
11	10366	1078	2077	3155	13521	22535	.77	.08	.15	.23	.30	.34	.66
12	10988	1039	2326	3365	14353	23922	.77	.07	.16	.23	.31	.31	.69
13	11530	977	2547	3524	15054	25090	.77	.06	.17	.23	.31	.28	.72
14	11990	868	2741	3609	15599	25998	.77	.06	.17	.23	.30	.24	.76
15	12382	813	2903	3716	16098	26803	.77	.05	.18	.23	.30	.22	.78
16	12725	735	3047	3782	16507	27512	.77	.04	.18	.23	.30	.19	.81
17	13016	636	3172	3808	16824	28040	.77	.04	.19	.23	.29	.17	.83
18	13265	592	3276	3868	17133	28555	.77	.03	.19	.23	.29	.15	.85
19	13481	501	3369	3870	17351	28918	.78	.03	.19	.22	.29	.13	.87
20	13660	438	3446	3884	17544	29240	.78	.02	.20	.22	.28	.11	.89
21	13811	369	3512	3881	17692	29487	.78	.02	.20	.22	.28	.10	.90
22	13933	293	3567	3860	17793	29655	.78	.02	.20	.22	.28	.08	.92
23	14039	299	3609	3908	17947	29912	.78	.02	.20	.21	.27	.06	.94
24	14131	217	3652	3869	18000	30000	.79	.01	.20	.21	.27	.06	.94
25	14301	220	3683	3903	18204	30340	.79	.01	.20	.21	.27	.06	.94
Totals	245808	16307	50222	66529	312337	520562	.79**	.05**	.16**	.21**	.27**	.25**	.75**

*Net assimilated energy, Kj.   **Ratio of totals.

50 females per ha or 81 males and 79 females per ha if only the area of less than 5 m water depth is considered. Moss Lake includes a surface area of 461 ha, 141 ha (30.6 per cent) of which has a water depth of less than 5 m.

Age distribution of males and females captured for the first time in the mark and release area during 1977 and 1978, the proportion that each age class was of the total sample, and the estimated number in each age class, (N_x), are given in Tables X and XI, respectively. Estimated age (N_x) distributions during 1977 and 1978 are shown in Figures 16 and 17 for males and females, respectively.

Energy consumed (C), assimilated (A), and produced (P, secondary production) by each age class and the total mark and release area population are given in Tables X and XI, for males and females, respectively. C, A, and P per ha for both sexes and the total population are given in Table XII, based on both the entire mark and release area (8.2 ha) and only the area of water depth of less than 5 m (5.2 ha).

The life table for Moss Lake P. scripta is presented in Table XIII. The M_x values were calculated from clutch size to PL relations (as presented above) and an assumed three clutches for all reproductive females (186 mm PL). These females were estimated to produce 4008 eggs per year during 1977 and 1978. Assuming a sex ratio of 1, an assumption supported by mark and recapture data and population

TABLE X

POPULATION DYNAMICS OF MALE Pseudemys scripta
IN MOSS LAKE MARK AND RELEASE AREA, 1977 AND 1978

Age Class	Observed				Estimated	
	N_{obs}	%	N_x	$C_x N_x$	$A_x N_x$	$P_x N_x$
0	0	0	0	0	0	0
1	0	0	0	0	0	0
2	0	0	0	0	0	0
3	0	0	0	0	0	0
4	5	1.6	7	13874	8323	791
5	15	4.8	20	52100	31260	2760
6	22	7.1	30	98250	58950	4890
7	32	10.3	43	171140	102684	8213
8	22	7.1	30	141600	84960	6690
9	22	7.1	30	164160	98490	7590
10	37	11.9	50	311500	186900	14250
11	17	5.5	23	160655	96393	7268
12	20	6.5	27	208899	125334	9423
13	16	5.2	22	186516	111914	8360
14	15	4.8	20	183960	110380	8160
15	12	3.9	16	158560	95136	7040
16	19	6.1	26	275028	165022	11908
17	10	3.2	13	145925	87555	6240
18	5	1.6	7	83076	49847	3570
19	12	3.9	16	199440	119664	8368
20	11	3.5	15	195195	117120	7905
21	1	0.3	1	13555	8133	542
22	3	1.0	4	56268	33760	2204
23	7	2.3	10	145450	87270	5550
24	3	1.0	4	59960	35976	2212
25	0	0	0	0	0	0
>25	4	1.3	5	80575	48345	2725
Total	310	100	419	3105686	1863416	136659

C_x = age specific comsumption

A_x = age specific assimilation

P_x = age specific production

TABLE XI

POPULATION DYNAMICS OF FEMALE Pseudemys scripta IN
MOSS LAKE MARK AND RELEASE AREA, 1977 AND 1978

Age Class	N_{obs}	Observed %	N_x	$C_x N_x$	Estimated $A_x N_x$	$P_x N_x$
0	0	0	0	0	0	0
1	0	0	0	0	0	0
2	20	6.2	25	70325	42200	7000
3	35	10.8	44	207548	124520	17996
4	37	11.4	47	322279	193358	26320
5	35	10.8	44	398068	238832	31064
6	23	7.1	29	325003	194996	24795
7	28	8.6	35	460845	276500	33250
8	30	9.2	38	570570	342342	40280
9	47	14.5	60	1143120	685860	154560
10	20	6.2	25	523125	313875	72475
11	15	4.7	19	428165	256899	59945
12	10	3.1	13	310986	186589	43745
13	10	3.1	13	326170	195702	45812
14	3	0.9	4	103992	62396	14436
15	3	0.9	4	107320	64392	14864
16	2	0.6	2	55024	33014	7564
17	2	0.6	2	56080	33648	7616
18	1	0.3	1	28555	17133	3868
19	1	0.3	1	28918	17351	3870
20	0	0	0	0	0	0
21	0	0	0	0	0	0
22	0	0	0	0	0	0
23	0	0	0	0	0	0
24	0	0	0	0	0	0
25	0	0	0	0	0	0
> 25	3	0.9	4	121360	72816	15612
Total	325	100.1	410	5587453	3352423	625072

C_x = age specific consumption

A_x = age specific assimilation

P_x = age specific production

Figure 16. Age distribution of male <u>Pseudemys</u> <u>scripta</u>
in the mark and release area. Age classes younger
than 6 y are not well represented presumably
because they have not moved into the mark and
release area. The arrow indicates age at matur-
ity.

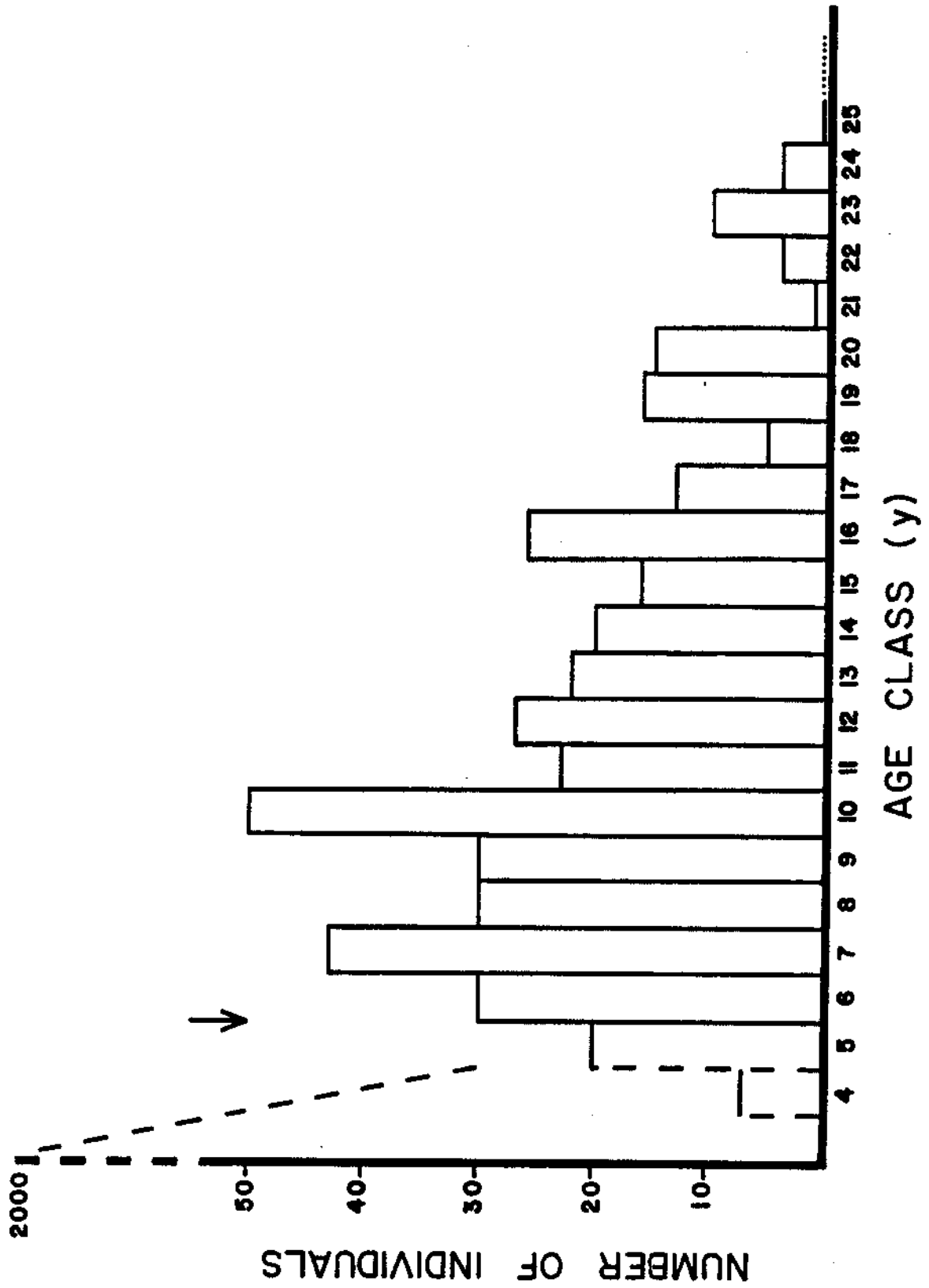Figure 16

Figure 16

Figure 17. Age distribution of female <u>Pseudemys</u>
<u>scripta</u> in the mark and release area. Symbols
are as in Fig. 16.

Figure 17
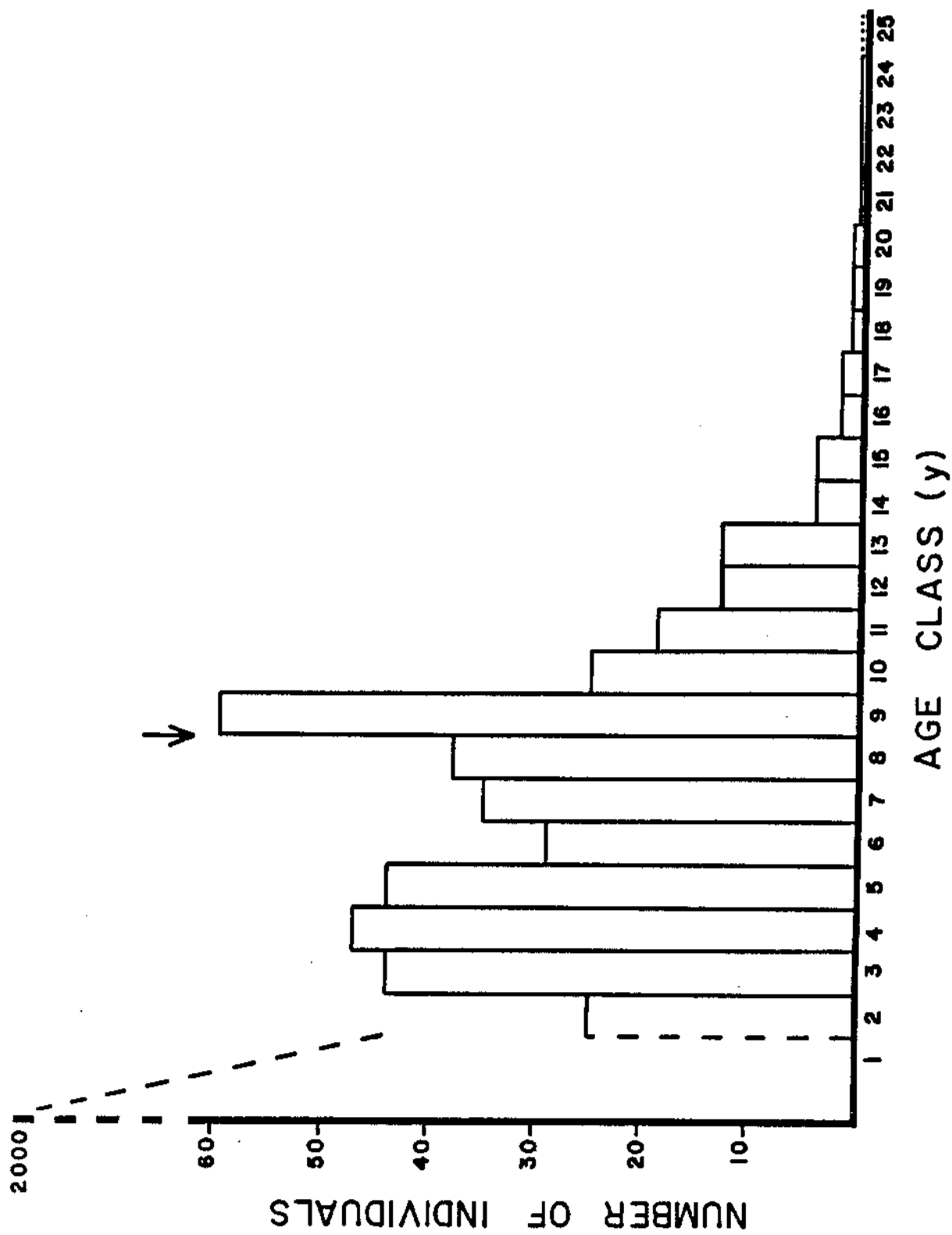
TABLE XII

POPULATION ENERGY FLOW IN MOSS LAKE Pseudemys scripta
IN THE MARK AND RELEASE AREA

	Male	Female	Total
Kj per mark and release area (8.2 ha)			
C	3105686	5587453	8693139
A	1863416	3352423	5215839
P	136659	625072	761731
Kj per ha			
C	378742	681397	1060139
A	227246	408832	636078
P	16666	76228	92894
Kj per ha, <5m water depth (5.2 ha)			
C	597247	1074510	1671758
A	358349	644697	1003046
P	26281	120206	146487

TABLE XIII

LIFE TABLE FOR FEMALE Pseudemys scripta IN MOSS LAKE
MARK AND RELEASE AREA, 1977 AND 1978

Age_x	N_x	M_x	$N_x M_x$	l_x	$l_x m_x$
0	–	–	–	1	0
1	0	0	0	–	0
2	25	0	0	–	0
3	44	0	0	.023	0
4	47	0	0	.023	0
5	44	0	0	.023	0
6	29	0	0	.02	0
7	35	0	0	.02	0
8	38	0	0	.02	0
9	60	23	1380	.02	.46
10	25	26	650	.013	.34
11	19	28	532	.010	.28
12	13	30	390	.007	.21
13	13	32	416	.007	.22
14	4	33	132	.002	.07
15	4	34	136	.002	.07
16	2	35	70	.001	.04
17	2	36	72	.001	.03
18	1	37	37	.0005	.02
19	1	37	37	.0005	.02
20	0	38	0	.0002	.008
21	0	38	0	.0002	.008
22	0	39	0	.0002	.008
23	0	39	0	.0002	.008
24	0	39	0	.0002	.008
25	0	39	0	.0002	.008
> 25	4	39	156	.0002	.008
Totals			N_o=4008		R_o=1.82

estimates for both sexes, approximately 2000 female eggs would be produced. This value is used as the beginning age class (N_O) in the life table.

CHAPTER VI

DISCUSSION

Age Determination

Pseudemys scripta in Moss Lake have extremely variable growth rates among years and age classes. However, their growth curve and the consequential age-size relationship are similar to age-size classes given by Cagle (1946) for P. scripta from Illinois. Growth of Moss Lake P. scripta is reasonably well described by the Van Bertalanffy growth model (i.e., growth decreases as a linear function of size). The model was effective in aging mature turtles. While the variation in size-specific growth rates makes aging an individual with certainty from its size tenuous, an expected age and variance limits can be determined.

The 95 per cent confidence limits relating age to PL are actually 95 per cent "best and worst" limits. The limits represent individuals that grow consistently at rates slower or faster than 95 per cent of all turtles, respectively. More realistically, most individuals experience periods of rapid growth and slower growth, which taken together over a long period are much closer to the mean and consequently, the 95 per cent confidence limits are actually narrower.

Though much of the variation in individual growth rates
is undoubtedly real, part may be an artifact of combining
short term and long term growth periods. Short term growth
measurements are especially sensitive to measurement error,
may include the disruptive effects of being captured, and
may over-emphasize particularly good or bad growth periods.
Growth is more rapid generally during the warmer midsummer
period than in the late spring and early fall (Cagle 1946).
Also, as supported by Cagle's (1946) work, turtle growth is
sensitive to local environmental conditions with,
individuals undergoing bursts of growth.

The inclusion of long term growth measurements may lead
to error in growth rate estimates due to individual
variation in the length of the growth period. Both Gibbons
(1967) and Ernst (1971a) found variation in the growing
season within a single population of *Chrysemys* *picta*. Some
turtles begin growth earlier in the spring and some continue
growth later in the fall than others. The assumption that
growth, measured between captures occurred between 1 April
and 30 September may be inaccurate. Consequently, the more
spring and fall periods that were included between captures,
the greater the potential error. Cagle (1946) concluded that
in Illinois the normal activity in mature P. scripta is
limited within the range of approximately 10 to 37°C. He
estimated the growing season to be from late April to early

October, a period he arbitrarily considered extending from 1
May to 1 October in Illinois. Cagle (1950) estimated this
period to begin about one month earlier in southern
Louisiana.

Most turtle growth studies have taken advantage of the
presumably annual growth rings on the scutes. However, since
this method is generally not practical to age mature
individuals, or at least older individuals, due to obscuring
of the rings, many studies have assumed a constant growth
rate after maturity. Wilbur (1975), working with Chrysemys
picta in Michigan, determined that juvenile growth can be
represented by a simple logarithmic function, but a simple
linear model best represents adult growth. He also suggested
that adults have varied annual growth and may cease growing
completely during unfavorable years. Gibbons (1968) assumed
a constant growth rate for adult C. picta in Michigan, but
suggested older adults probably grow more slowly than
younger adults. Cagle (1946) found that growth in adult P.
scripta in Illinois was variable and was progressively
slower with an increase in size.

Metabolic Heat Loss

Estimated field metabolism is a tenuous component of
the energy budget. Metabolism has not been reported in free
ranging turtles. Estimating field metabolic rates from

resting laboratory rates should be considered an approximation.

Assuming that turtle temperature is equal to water temperature is realistic for the period during which water temperature is below 20°C and above 30°C. During these periods turtles seldom bask. Some individuals do bask at any time during the winter when conditions are appropriate (several consecutive days of warm, sunny weather) and can raise their body temperature above the water temperature for short periods. However, the effect of winter basking on the annual metabolism probably is negligible, because the basking periods are short and infrequent and the heat gained is lost rapidly when the turtles enter the water. Summer aerial basking (when water surface temperature is greater than 30°C) is restricted to early mornings. Since the preferred temperature in P. scripta is approximately 30°C (Gatten 1974), turtles probably are capable of maintaining thermal requirements within the water column.

During the spring and fall when water temperature is changing between 20 and 30°, water temperature is not a reliable estimator of turtle body temperature. Turtles spend much more time basking aerially and can effectively maintain higher body temperatures during this time (Boyer 1965). The water temperature is between 20 and 30°C in Moss Lake for approximately 40 days in the spring and 40 days in the fall,

a period that is almost half of the activity season. Cagle (1946) concluded that in Illinois, the normal activity in mature P. scripta is limited within the range of approximately 10 to 37°C.

Production

In general, Moss Lake P. scripta growth rates are similar to those of other mainland temperate latitude P. scripta in habitats that are not artificially heated (Gibbons et al. 1979, Gibbons et al. 1981, Thornhill 1982). Also, the growth pattern is similar to other P. scripta, and many other turtle species studied, in that growth is most rapid in smaller individuals and slows drastically at maturity. However, considerable variation in growth rates has been recorded, both within and between populations (Cagle 1946, Gibbons et al. 1979, Gibbons et al. 1981, Thornhill 1982). Table XIV lists available data on age-size relations in P. scripta.

Growth rate estimates for immature Moss Lake turtles are lower than estimates of other populations based on age at maturity estimates. There are several possible factors that could account for this: (1) The point at which turtles are assumed to begin their lives varies among workers. Some workers (Gibbons et al. 1981, present study) have assigned an age of 1 y to turtles at the end of the season in which they were hatched, so that turtles enter their first full

TABLE XIV

AVAILABLE DATA ON AGE-SIZE RELATIONS
IN Pseudemys scripta

Source	Locality	Male Age(y)	Size(mmPL)	Female Age(y)	Size(mmPL)
Webb 1961	Lake Texoma, Oklahoma	4*	89**, 90-100**	4*	145**, 174-193**
Gibbons 1981	Par Pond N.C. Ellenton Bay N.C.	3-4, 4-5	100-120**, 90-110**	8, 8	195-210**, 160-175**
Cagle 1946	Ill., Tenn., Louisiana	2-5*	90-100**	2-10	150-195**
Avalos 1975 in Thorn-hill 1982	Lake Baldwin, Randolph and St. Clair Co., Illinois			3*, 4	183.5, 206.5, 186**
	Natural Areas near Lake Baldwin			3*, 4	144, 175, 180**
Present Study	Moss Lake, Cooke Co., Texas	4, 5, 10	74, 84, 126	4, 8, 10	123, 178, 194**
Moll and Legler 1971	Rio Chagres, Canal Zone, Panama	2-3*	125-135**	6-8*	240-260**

*Season of hatching not included in age.
**Size at maturity.

season at an age of one. Other workers (Cagle 1946, Webb 1961, Moll and Legler 1971, Avalos 1975) have assigned an age of 1 y at the end of the turtle's first full season of growth, which would be equivalent to an age of 2 y in the previous aging scheme; (2) There is evidence (Cagle 1946) that turtles may grow much more rapidly in their first several years than during the rest of their immature years. Little data are available on first and second year Moss Lake turtles, and a linear decrease in growth rate with size is assumed. This could lead to a slight overestimate of age with size.

The energy densities of Moss Lake P. scripta carcass, fat and eggs are similar to those reported for other reptiles. The differences in egg values are notable, possibly resulting from different lipid contents and relative shell masses. Chrysemys picta eggs with the shell removed have approximately the same energy density as ash-free Moss Lake P. scripta eggs, even though the lipid content is slightly higher in P. scripta, 25.8 compared to 22.0 per cent of total dry egg mass (Congdon and Tinkle 1982). However, the estimated energy density of Malaclemys terrapin eggs (shell included) is considerably higher than P. scripta eggs (ash included) even though the lipid consent is similar, 26.4 and 25.8 per cent, respectively (Ricklefs and Burger 1977).

While energy density of each lipid-free component is fairly constant with increase in body size, the energy density of the total dry lipid-free body mass (DLFM) is not. In both males and females, the per cent of the total DLFM that the shell DLFM comprises increases considerably while the carcass DLFM per cent decreases. In males, the shell DLFM increases from approximately 43 per cent at 70 mm PL to about 77 per cent at 200 mm PL. In females, the shell DLFM increases from approximately 50 per cent at 70 mm PL to about 80 per cent at 230 mm PL. Since the energy density of carcass DLFM is more than twice that of shell DLFM (Table V), the energy density of the non-lipid portion of the turtles decreases with size. Therefore, unit increases in size are less energetically expensive, ignoring the energy required to produce and maintain the biomass, as size increases. For example, a gram of total DLFM of a 70 mm PL turtle contains approximately 13.5 Kj compared to approximately 10.5 Kj for an adult turtle (190 mm PL).

In males the proportional increase of DLF shell to total DLFM with PL is close to linear, while in females there is a sharp increase until a PL of 130-150 mm is reached, and then a slow increase. The relative DLFM of the shell of 4 to 6-y females is close to that of old adults. However, the weight of the DLF shell increases with PL at about the same rate in both sexes, so that both sexes have

shells of similar weights at a given PL. The shift in proportional shell weight (shell to total DLFM) may reflect an ontogenetic change in geometry of females that occurs prior to maturity. Females have higher, more dome-like shells than males, in relation to PL, a shape that accommodates a larger body cavity. Both clutch size and egg size increase significantly with PL in P. scripta, characteristics that are influenced by the size of the body cavity.

Iverson (1982a) found that in Chrysemys picta in Nebraska, the per cent dry skeletal mass to live body mass and carapace length increased with body size at about the same rate in both sexes, then abruptly slowed at approximately the same body size in both sexes. The body size of the shift is the size of maturity of males but much smaller than the size of maturity of females. The proportion of the skeletal mass that the shell constitutes however, is not discussed.

Bertl and Killebrew (1983) found that in Graptemys versa and G. caglei there is little increase in shell weight with carapace length below 60 mm, the approximate size of maturity. They suggested that "before sexual maturity, turtles are growing faster in size than after sexual maturity, when they add thickness to the shell".

Lipid stores represent a biochemically efficient mechanism for storing energy and, in many reptile species, are an important source of large quantities of energy, produced when conditions are favorable, then used later when conditions are unfavorable (brumation) or when larger quantities of lipids are needed (vitellogenesis) (Derickson 1976). To estimate energy partitioning, it is necessary to know how stored lipids are ultimately used. For example, lipid produced in the summer, stored over winter, then used the following spring to produce yolked ova should be considered as energy devoted to reproduction. The noncyclic structural lipids, however, that increase in mass as body mass increases should be considered as energy devoted to secondary production (Pg).

Young Moss Lake female P. scripta (<100 mm PL) have very little total extractable lipids (TDLM). Between 100 and 180 mm PL, the total lipids increase at a uniform rate (in turtles sampled from different times of the year) to approximately 40 g dry lipid mass (DLM). Beyond 180 mm PL (maturity), the total lipid content is extremely variable, ranging from 40 to 145 g DLM. Lipid in the carcass and viscera is the most variable while the shell lipid is somewhat more constant.

The extreme variation in lipid mass in mature females suggests that lipids are stored and then depleted, as would

be expected, but the cyclic pattern is not clear. Turtles collected during early fall just before the end of the activity season (fall turtles) generally had a greater lipid mass than females collected in the early spring just prior to ovulation of the first clutch of eggs (early spring turtles), late spring just after ovulation of the first clutch (late spring turtles), and summer after egg production is complete (summer turtles). The difference between fall and early spring turtles and between early spring and summer turtles, however, is not significant (P>0.05). Absence of significant differences results in part from small sample sizes, but still the large amount of variation obscures a pattern in lipid cycling.

The DLM to PL relationship is similar in Moss Lake males except adult males had lower variability. Juvenile males had almost no lipids, then at approximately 100 mm PL the LDM began increasing at a fairly constant rate.

Congdon and Tinkle (1982), working with Chrysemys picta in Michigan, found a similar lack of lipid cycling pattern. Although total lipid levels decreased during the period between spring emergence and the nesting season, the difference was not significant. The energy equivalent in the mean lipid reduction, however, was 47 per cent of the energy of an average clutch.

Derickson (1976) stressed that "food availability, including an organism's access to its food supply, is the ultimate factor that determines (1) whether or not an organism stores lipids, (2) when an organism stores lipids, (3) the quantity of lipid that is stored and (4) for what purpose the stored lipids are used". If food is available seasonally, lipids should be stored and then utilized later, producing a seasonal pattern. The quantity and timing of lipid storage should be determined by the level and duration of food availability, in relation to the timing and level of energy demands. If food is typically available for a short period of time, at a time other than when a large quantity of energy is required, a pattern of lipid storage and depletion should develop.

Aquatic vegetation, a primary food of Moss Lake P. scripta, is available most of the year in Moss Lake. Studies of P. scripta food habits in South Carolina (Clark and Gibbons 1969, Parmenter 1980) and examination of stomach and gut contents of those in Moss Lake suggest P. scripta, though opportunistic, are generally herbivorous. Utilization of plants, however, is limited primarily by water temperature which affects ingestion and digestion rates. Parmenter (1980) found that the ingestion rate in P. scripta increases more than threefold between 20 and 30 $^{\circ}$C, the maximum ingestion rate occurring at 29°C. Parmenter (1981)

found that digestive turnover rates of bologna in <u>Chrysemys</u> <u>picta</u> and <u>P. scripta</u> were 59 and 61 h, respectively, at $25^{\circ}C$, but was only about 30 h in <u>C. picta</u> at $30^{\circ}C$.

Moss Lake <u>P. scripta</u> have a food source limited by physiological constraints. The time required to harvest and process the food may be of primary importance. Turtles are active when the water temperature is above $20^{\circ}C$ and are capable of ingesting and digesting food during this time, although both processes are greatly enhanced as the water warms and conditions permit at least short periods of elevated body temperatures by aerial basking. Many adult turtles enter the inactive period with developing ovarian follicles 10-15 mm in diameter. These follicles are as much as a fourth of the volume of the first clutch which is ovulated in May at a diameter of about 25 mm. Moss Lake <u>P. scripta</u> become active in early April and therefore have more than a month to assimilate the energy required to complete the first clutch of eggs without heavy reliance on stored lipids. Lipids possibly are depleted only in exceptionally bad years.

Total DLM is included as a component of body growth (Pg) in Moss Lake <u>P. scripta</u>, and the DLM to PL relation is used to estimate size-specific increase in DLM. This method ignores the use of stored lipids for metabolic heat production or egg production in future years, and therefore

leads to an underestimate of energy devoted to R and Pr and an overestimate of the energy devoted to Pg. In an adult female, the estimated amount of DLM contains approximately 50 per cent of the energy contained in the estimated total DLFM and 66 per cent of the annual reproductive output.

Reproduction in Moss Lake P. scripta is similar in most aspects to reproductive characteristics of other populations of P. scripta studied. As with Moss Lake turtles, clutch size has been positively correlated to body size in all studies except Webb's (1961). However, he examined only six females that ranged in PL from 180 to 230 mm, and, consequently, his results may have been an artifact of small sample size.

Gibbons (1970b) and Gibbons et al. (1981) found that P. scripta in certain habitats that receive heated effluent (Par pond on the Savannah River Plant, South Carolina) have higher growth rates, larger size at maturity and larger clutches than nearby populations in normal habitats. Larger body size and large clutch size was also found in P. scripta populations on several South Carolina barrier islands (Gibbons et al. 1979). Congdon and Gibbons (1983) demonstrated, however, that many of the reproductive traits (clutch size, clutch wet mass, egg wet mass, and egg width) in both large and small body size female P. scripta are associated with body size. They further demonstrated that

these reproductive attributes are not significantly different when the effect of size is removed, and therefore the investment per egg and per clutch, proportional to body size, remains essentially constant.

Assuming that all mature females produce three clutches possibly overestimates the average realized reproductive output in Moss Lake P. scripta. However, all females dissected had some combination of large yolked ovarian follicles, corpora lutea and oviducal eggs, indicating that she had or would produce three clutches. Gibbons (1982) found that while the clutch size within an individual P. scripta in South Carolina does not vary between years, the clutch frequency does. Congdon and Tinkle (1982) and Tinkle et al. (1981) found that clutch frequency among individuals in a Michigan Chrysemys picta population is variable, with approximately 10 per cent producing two clutches and 30-50 per cent not reproducing. The assumed reproductive output in Moss Lake P. scripta certainly is near the maximum, characteristic of a rapidly expanding population (see comments below).

In Moss Lake P. scripta, the mean egg dry mass increases significantly with body size (PL), increasing more than one-third over the size range of mature females. For example, a 20-year-old female could increase the number of eggs she produces annually, from approximately 37 to 53,

with no change in energy requirements, by producing eggs the
size of a 10 year old female (assuming three clutches per
year). The egg size to body size relation in turtles is not
as clear as the clutch size to body size relation. Cagle
(1950) and Webb (1961) reported no correlation of egg size
to PL in P. scripta, while Moll and Legler (1971) reported a
decrease in egg length with clutch size. Egg wet mass and
egg width were found to increase with body size in P.
scripta (Congdon and Gibbons 1983) and Deirochelys
reticularia (Congdon et al. 1983). Congdon and Tinkle (1982)
found a correlation of egg width and pelvic opening width to
carapace length in Chrysemys picta and suggested that pelvic
opening width may place a constraint on maximum egg size in
this species.

Energy Budget

The level of energy utilization is dependent on the
diet, time-activity patterns and thermal constraints of Moss
Lake P. scripta. Many aquatic macrophytes have an energy
content of about 17 Kj g^{-1} dry mass (Boyd and Goodyear
1971), about 10 Kj g^{-1} of which is assimilated by turtles
(if the assimilation efficiency is 0.6, see comments above).
The per gram energy requirement (assimilated) decreases with
increasing live body mass, ranging from 18 to 9 Kj (gLBM
y)$^{-1}$ in 1 to 25 year old individuals, respectively, of both
sexes. A moisture content of about 93 per cent in aquatic

macrophytes (Boyd 1968), digestive turnover rates of about 24 h at 30°C (Parmenter 1981) and a period of about 125 days of water temperature near 30°C would require that turtles eat a mass of aquatic vegetation equivalent to about 20 per cent in juveniles and 10 per cent in large adults of their live body mass daily.

The nutritional level of the food and the length of time available for feeding are both underestimated. The inclusion of plant parts with higher energy densities, such as seeds, invertebrates, and possibly microbial colonies associated with aquatic vegetation in the diet would increase the energy consumed and the proportion of food ingested that is assimilated. If intestinal fermentation occurs in turtles as in some iguanine lizards (Iverson 1982b), the assimilation efficiency would be increased. Behavioral thermoregulation, primarily aerial basking, enables turtles to extend seasonal activity, permitting some feeding during the period turtles are assumed to be inactive (October - March).

Since energy devoted to reproduction in Moss Lake P. scripta is measured only as chemical energy in eggs of females, energy devoted to reproduction is underestimated, perhaps by more than 50 per cent. Nagy (1983) estimated that in free living Uta stansburiana, the energy metabolism required to produce eggs is greater than the potential

chemical energy in those eggs, 130 and 180 per cent in first and second year females, respectively. He further estimated that, in males, the energy devoted to reproduction, the metabolic cost of activity related to reproduction, is approximately one-half the total reproductive cost in females. The metabolic cost related to reproduction in P. scripta, however, was not measured and was included in total metabolic heat loss (R).

Male and female P. scripta reproductive tactics are responses to different sets of selective forces and are reflected in their different energy utilization patterns. Berry and Shine (1980) demonstrated the correlation of sexual size dimorphism with habitat type and male mating strategy. In species in which females are forcibly inseminated or males engage in combat with other males, males typically are larger than females. However, in species in which males utilize elaborate precoital displays and female choice is highly important, as in P. scripta, males are usually smaller than females. Ghiselin (1974) further proposed that if a male's fitness is increased by locating and inseminating the largest number of females, then selection may favor more mobile males. Smaller males may be more energetically efficient than larger males, and therefore able to devote more of the available energy into locomotion than growth. Increased searching time, however,

may also increase exposure to predation and reduce the time available to thermoregulate.

Moss Lake male P. scripta reach sexual maturity in their sixth year, a point at which the proportion of energy devoted to growth (Pg/A) decreases and becomes essentially uniform for the rest of the turtle's life. The size obtained by males in about their sixth year may be the size at which they are somewhat immune to many predators, and the advantages of devoting energy to reproductive activities outweigh the advantages of devoting energy to growth. Growth in males is more erratic than in females, and maximum male live body mass is about one-half that of females, indicating that increases in adult size is less of a selective advantange in males than females.

Courtship occurs in the spring prior to nesting (Ernst and Barbour 1972), and males maintain a constant search for females during daylight hours (Cagle 1950). Though water temperature in Moss Lake is below 30°C during this period, basking enables turtles to maintain higher body temperatures. However, time spent searching should reduce basking time and, ultimately, digestive rates and the quantity of energy assimilated.

Reproductive effort (RE) of female Moss Lake P. scripta (16 to 20 per cent), defined as the portion of assimilated energy devoted to reproduction (Pr/A), is similar to other

reptiles in which RE was measured as a proportion of assimilated energy. Tinkle and Hadley (1975) tentatively estimated that 10 to 24 per cent of assimilated energy was devoted to reproduction in three lizard species (Sceloporus jarrovi, a live bearing species 10 to 13 per cent; Uta stansburiana, an egg laying species, 19 per cent; and Sceloporus graciosus, an egg laying species, 23-24 per cent). Nagy (1983) estimated in female Uta stansburiana, 13-16 per cent of assimilated energy is devoted to eggs, but about 35 per cent of assimilated energy is devoted to total reproduction (eggs and metabolic cost to produce eggs). Smith (1976) estimated that as much as 81 and 86 per cent of assimilated energy was devoted to reproduction in two snake species, Heterodon platyrhinos and Elaphe guttata, repectively, maintained in the laboratory.

Congdon et al. (1984) estimated RE in Chrysemys picta in Michigan as about 14 per cent annually in 8 to 14-y females and about 10 per cent over the 14-y life span (calculated as ratio of total energy invested in eggs to total lifetime assimilated energy, Table IV, Congdon et al. 1984).

The similarity of RE in Moss Lake P. scripta, a late maturing and long lived species (16-20 per cent), to RE values reported for lizard species, early maturing and short lived species in relation to P. scripta, is surprising.

However, the similarity of clutch size to body size relations and maximum reproductive potential in North American P. scripta populations (Congdon and Gibbons 1983), indicates similar RE in terms of female body to clutch biomass. The observations of Congdon and Tinkle (1982) and Gibbons (1982) that the clutch frequency is more variable than the clutch size in Michigan Chrysemys picta and South Carolina P. scripta, respectively, suggest that RE may vary widely among populations of turtles. As suggested by Gibbons (1982), clutch frequency is probably much more important than clutch size or egg size in determining RE. The production of three clutches annually by many Moss Lake P. scripta, if accurate, would then represent a near maximum level of RE for North American populations of P. scripta, assuming maintenance and growth requirements are similar.

Wilbur et al. (1974) stressed that lowering reproductive effort, in an environment where juvenile mortality is high and adult mortality is low, would produce no selective advantage unless it increased the lifetime reproductive success. Further, they pointed out that if females could predict the juvenile success in an upcoming period, they could adjust their RE accordingly. In an environment where breeding more strongly decreases adult survival or a period of low juvenile survival is predicted, reproductive effort should be lower. If movement onto land

to nest is a particularly dangerous endeavor, reducing the number of nesting trips (clutches) during a breeding season, rather than clutch size or egg size, may have the greatest effect on lifetime reproductive success.

Even though the demographic environment may be a primary selective force in determining RE in turtles, the level of RE among populations may vary considerably. The prediction following this is that RE among populations should be more closely correlated to female nesting mortality than to resource level.

The variation in clutch size (cv=23) in Moss Lake turtles is less than the variation in total dry lipid mass (TDLM) for all mature females (cv=37), mature fall females only (cv=32), mature early spring turtles only (cv=44) and mature summer turtles only (cv=42). Assuming three clutches in all mature females, the variation in annual reproductive output would be similar to variation in clutch size. Some turtles have relatively large lipid deposits, which presumably could be used to produce eggs, yet produce clutches similar in size to those of females with smaller lipid deposits. Greater variation in energy reserves, and presumably potential reproductive output, than actual reproductive output suggest that RE in Moss Lake turtles is not primarily a response to available resource level. The level of RE may be a bet-hedging strategy, demographic

environment being a primary selective force. The demographic data are not available to test this contention, however.

Congdon and Tinkle (1982), considering the complexity of reproductive energetics in Chrysemys picta, suggested that an annual energy budget may not be appropriate. The use and timing of stored body lipids in reproduction coupled with varying clutch frequency makes placing reproductive energetics into a discrete annual energy budget difficult. These authors suggest that "RE in C. picta, and possibly all long-lived animals, will be best explored in terms of a lifetime energy budget".

A typical female Moss Lake P. scripta devotes 16 per cent of the energy she assimilates to eggs (RE) during her 25-y life span. RE increases sharply from the first reproductive season for approximately 5 y, at which point it begins to level. If energy required for maintentance is reasonably stable, in relation to body size, then measuring the partitioning of "extra" energy may help to understand the selective forces shaping RE. After sexual maturity the proportion of energy devoted to secondary production, (Pg + Pr), remains essentially constant. The increase in RE coincides with a decrease in energy devoted to growth (Pg). The proportion of secondary production devoted to reproduction (Pr/P) increases at nearly a constant rate over the adult life of a female. The lifetime Pr/P is

approximately 75 per cent. Both RE (=Pr/A) and Pr/P change more rapidly per year in younger adults than in older adults.

Population Dynamics

The crude and ecological density estimates (101 ha^{-1} for the entire cove and 160 ha^{-1} for the area less than 5 m deep) for P. scripta in the mark and release area of Moss Lake is somewhat higher than that reported by Gibbons (1970a) (88 ha^{-1}) for a P. scripta population in a 10-ha Carolina bay in South Carolina. Density estimates for Chrysemys picta populations include 99 to 410 ha^{-1} depending on water level (Sexton 1959b Michigan), 576 ha^{-1} (Gibbons 1968 Michigan), and 590 $^{-1}$ (Ernst 1971b Pennsylvania).

Although some immigration and emigration occurs in the mark and release area, the net effect probably is minimal. Trapping marked turtles throughout the lake supports this. Thirty six turtles were trapped, marked and released in several coves along the shore of the North Fish Creek arm of the lake, approximately 0.9 to 1.6 km from the mark and release area, where five were recaptured within 2 y and a total of 873 trap hours. Of 290 turtles marked in other areas of the lake, mostly the west end approximately 5 km by the most direct aquatic route, only four were recaptured in the mark and release area after 4 y and a total of 1327 trap

hours. Only six turtles from the mark and release area were recaptured in other parts of the lake during 2 y.

Age distribution within the mark and release area was similar for both sexes with some notable differences. Small juveniles, less than 75 mm PL (less than 4 y males and 2 y females), were not seen basking or foraging and were not trapped in the mark and release area. Numerous juveniles of both sexes larger than 80 mm PL were collected. Because the 2.5-cm mesh traps, set in a similar manner in other localities, have trapped small juveniles, the lack of this size class in the mark and release area was assumed to be not entirely the result of trapping bias. Turtles apparently spend their first several years in other habitats, then move into more open water when they obtain a size of about 80 mm PL. This is possibly a size at which they are less vulnerable to predation in the more open water.

In both sexes, age classes up to the ninth or tenth year are well represented, with older age classes becoming increasingly more scarce. The decrease is more apparent in females than males. Since males mature earlier and at a much smaller size than females, the juvenile to adult ratio is considerably different. Of the turtles present in the mark and release area, about 93 per cent of the males were mature while only about 36 per cent of the females were mature. The sex ratio however, is very close to one.

Age distribution is related to recent habitat modification experienced by this population. Moss Lake was formed by impounding Fish Creek in 1966. Turtles older than 10-12 y represent the original creek population and possibly those from nearby stock tanks. The vastly expanded aquatic habitat has been beneficial to the turtle population, especially after the water level stabilized and aquatic vegetation became established. The large proportion of turtles less than 12 y (78 per cent) and the sharp decrease in the number in the older age class turtles very likely is the result of the formation of the lake. The females of the first lake cohort are becoming sexually mature (about 9 y) and beginning to reproduce, the demographic consequences of which should be a large increase in the number of eggs produced. The population present in 1977 and 1978 may be in the early stages of considerable population growth. The net reproductive rate (Ro=1.8) indicates nearly a doubling of the population per generation (11.5 y). The predicted survival rates for adult turtles are considerably underestimated due to an assumption of an initial size of 2000 eggs for each cohort. However, the fecundity schedule is a maximum estimate. If the realized reproductive potential approaches this estimate, as the sample of dissected females indicates, the population is increasing.

The maximum age of Moss Lake P. scripta is about 25 y. Although two males, estimated to be 30-35 y old and two females estimated to be over 35 y old were collected, most turtles (99 per cent) were less than 25 y old. The few turtles estimated to be over 25 y may actually be individuals that have experienced exceptional growth and consequently were not accurately aged. The older individuals are remanants of the creek population present before the formation of Moss Lake; the effect of the lake habitat on the life span of the turtles can not be determined until turtles that have spent their entire lives in the lake constitute the older age classes.

If the Moss Lake P. scripta population is indeed increasing, the energy flow rates will increase similarly. The energy dynamics of turtles are functionally more related to body size than to age (Wilbur 1975, Bennett and Dawson 1976). Consequently, the estimate of the energy dynamics should be independent of errors involved in age determination. The age distribution of Moss Lake turtles is actually a more accurate measure of size than age, since age distribution was based on size. The effects of body size distribution and population size on energy dynamics are profound.

The assessment of population density, and consequently energy flow rates per area, is complicated by diverse

habitat in Moss Lake. Although turtles in Moss Lake undoubtedly swim in deeper water, they essentially exploit only the area of less than 5 m depth. Their food source (aquatic vegetation and associated animals) is restricted to this area and the thermal mosaic (including aerial basking sites and water column temperature profile) necessary to maintain body temperature requirements is available. Estimating density for the area of shallow water (less than 5 m) is biologically realistic for the Moss Lake population (i.e., ecological density).

Estimating survivorship as the number observed in each age class in relation to the calculated egg production of the population requires the assumption that egg production has remained similar over previous years. This assumption can not be supported in the Moss Lake P. scripta population and, coupled with the variance in the age determination of an individual from the age-size relation, makes the calculation of a precise life table tenuous. However, certain characteristics of the life table can be approximated and are important in understanding the demographic environment.

Juvenile survival (including eggs, hatchlings, and juveniles until they enter the mark and release area at about 3 y old) was low. An estimation of 2000 female eggs, based on every adult female producing three clutches per

year, is close to the maximum reproductive potential for the
population probably for any year since the formation of the
lake. In order to estimate the minimum initial size of the
1977-1978 3-y age class, and therefore the maximum survival
rate, all females that had been mature for 3 y or less were
excluded (this method ignores the loss of older females
during the three years) and only one clutch per female was
assumed. The minimum reproductive potential was about 240
female eggs. The survival rate to 3 y then ranged from about
2 to 18 per cent. Tinkle et al. (1981), in one of the few
studies where egg and hatchling survival have been measured
directly, determined that about 67 per cent of a Michigan
population of Chrysemys picta eggs survive the first year
and have a 76 per cent survival rate thereafter, so that
about 39 per cent survive to 3 y.

The Moss Lake P. scripta population is a growing
poulation, in response to greatly increased aquatic habitat.
With a net reproductive rate of 1.8 and generation time of
11.5 y, the population should double in 10-15 y. The
population is characterized by a high reproductive output
(24-40 eggs per year per female), low juvenile survival
(2-18 per cent to 3 y), and a maximum age of approximately
25 y. The lack of stable age distribution, resulting from
disproportional increases in younger age classes originating
in the lake, complicates the calculation of demographic
statistics.

CHAPTER VII

CONCLUSIONS

(1) During the life of the typical Moss Lake P. scripta
male, 93 per cent of net metabolizable energy is lost
through metabolic heat production and 7 per cent is devoted
to growth. The typical female proportions 79 per cent to
metabolic heat production, 5 per cent to growth and 16 per
cent to egg production. Storage, total somatic lipids, is
highly variable within and among seasonal samples and,
consequently, no cyclic pattern of accumulation and
depletion is evident.

(2) Female RE, the proportion of available energy devoted to
egg production, increases from 13 per cent in the first
reproductive year to 20 per cent in older individuals.
Lifetime RE is 16 per cent. The level of RE in Moss Lake P.
scripta is similar to RE values reported for short lived
lizards and another turtle, Chrysemys picta.

(3) No seasonal pattern is evident in lipid storage and
utilization although considerable differences in lipid
levels among individuals suggests that lipids are

accumulated then depleted. Reproductive output is less variable than lipid levels during any season (early spring, late spring, summer or fall) indicating that resource level is not the primary factor determining reproductive output.

(4) The mark and release area supports about 831 turtles with a sex ratio of one. This area is 8.2 ha, 5.2 ha of which has a water depth of less than 5 m. The population is a growing population in response to the formation of the lake which greatly increased the aquatic habitat suitable for turtles. Energy consumed, assimilated and produced annually is estimated from the age specific energy budgets, population density and size distribution estimates.

(5) Considerable variation in growth rates, and consequently variation in the size-age relation, coupled with an unstable age distribution, has complicated calculation of a survivorship schedule. However, certain characteristics of the life table can be approximated. Juveniles have a low survival rate of 2-18 per cent, the generation time is about 12 y and maximum age is about 25 y. With a net reproductive rate of 1.8, the population should double in 10-15 y.

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