VARIATION IN THE LIFE HISTORY

OF NOTURUS EXILIS NELSON

By

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PREFACE

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I would like to thank my grandparents, Mr. and Mrs. Amos L. Bloom, for providing financial support and lodging for many collecting trips.

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CHAPTER I

INTRODUCTION

The two phrases "life history study" and "life history theory" represent contrasting thoughts and ideas. A life history study reveals information on feeding, reproductive, and demographic characteristics whereas life history theory attempts to describe cause and effect patterns in nature. Rarely are the two approaches combined.

When the two approaches are combined, patterns obtained for one species are frequently applied to other organisms. This limitation is necessary because although certain vertebrate groups have been studied extensively (e.g. lizards and birds), detailed life history data is lacking on the majority of organisms. This lack of information inhibits the development of comprehensive theories. In addition, the data that are available do not combine a cause and effect approach.

Ideally a life history study would consist of intensive observations of a population, coupled with direct manipulation of relevent variables making up a life history strategy. Stearns (1976a) outlined the difficulties in this type of study. One major problem is that turnover time in vertebrates makes this approach difficult although commendable attempts have been made on invertebrates (Barclay and Gregory, 1981). An alternative approach is to study different populations of the same species in different locations. Observable differences in life history characteristics can then be followed by a

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quantitative analysis of differences in the locations that might reveal patterns that support or refute theoretical predictions. Geographical variation in life history characteristics has been observed in many fish species (Hubbs, 1958; Hubbs and Johnson, 1961; Carscadden and Leggett, 1975), but mechanisms underlying such variation are seldom clear (see Reznick and Endler, 1981 for an exception).

Evolutionary theory assumes that populations are selected so that life history strategies are tailored to the environment. Therefore, populations subjected to a similar set of environmental variables should have similar life history strategies. MacArthur and Wilson (1967) were among the first to use these assumptions to explain life history strategies. They coined the terms r- and K-selection to explain adaptation in variable and constant environments, respectively. I use the terms r- and K-selection as shorthand for density independent selection and density dependent selection, respectively. Pianka (1970) explained these terms as endpoints on a continuum, which implies that populations occupying slightly different environments would never be located at the same point on this ecological gradient.

The r- and K-selection model often is inadequate to explain observed life history patterns (Wilbur, Tinkle, and Collins, 1974). Therefore other approaches have been proposed. Recently a model called "bet-hedging" has been recognized (Stearns, 1976a). Stearns (1976a) summarized bet-hedging as follows:

> A fluctuating environment that has its impact on juvenile mortality favors reduced reproductive effort, smaller clutches, and longer-lived organisms. But environmental variability that affects adult survival favors increased reproductive effort, larger clutches, and short-lived organisms (p. 25).

Components of this model have been reported by Murphy (1968), Schaffer (1974), Schaffer and Elson (1975), Leggett and Carscadden (1978), and Woodward (1982). It is obvious that these two models can give different predictions for life histories at any given location. Table I lists and contrasts the predictions of bet-hedging with those of r- and K-selection. The utility of these models depends on how well they predict reality.

It is toward this evaluation that this study is directed. I examined life history characteristics of three different populations of Noturus exilis, the slender madtom. The three populations were compared to determine if differences in geographical and climatic conditions could explain any differences in life histories among the populations. Climatic predictabilities were calculated using Colwell's (1974) equations. The patterns found in N. exilis were compared to the differing predictions outlined in Table I.

TABLE I

THE CONTRASTING PREDICTIONS OF R- AND
K-SELECTION AND BET-HEDGING

1) r- and K-Selection and Bet-hedging With Adult Mortality Variable

Stable Environments	Fluctuating Environments
Slow Development and Late Maturity	Rapid Development and Early Maturity
Iteroparity	Semelparity
Smaller Reproductive Effort	Larger Reproductive Effort
Fewer Young	More Young
Long Life	Short Life

2) Bet-hedging With Juvenile Mortality Variable

Early Maturity	Late Maturity
Iteroparity	Iteroparity
Larger Reproductive Effort	Smaller Reproductive Effort
Shorter Life	Longer Life
More Young Per Brood and Fewer Broods	Fewer Young Per Brood and More Broods

Source: Stearns (1976a).

CHAPTER II

LITERATURE REVIEW

Life History Data

Good review papers on life history theory are available (Stearns, 1976a, 1977). These papers deal with the development of life history theory and review work on r- and K-selection and bet-hedging. Several studies support the hypothesis that r- and K-selection occurs. Stearns (1976b) compared populations of Poecilia reticulata and Gambusia affinis in fluctuating and nonfluctuating Hawaiian reservoirs and found eight of nine reproductive variables showed trends predicted by r- and K-selection. Seven of these trends, however, were statistically insignificant. In addition to this study, some authors have reported ecological results. For example, Constantz (1979) contrasted populations of Poeciliopsis occidentalis in a spring versus fluctuating desert wash and found that patterns of reproductive effort and generation time did not fit predictions of r- and K-selection, but that growth and investment of offspring did.

A few published examples exist which support the hypothesis of bet-hedging. Katz (1948) and Paulson and Smith (1977) found that herring (Clupea pallassii) of the same size class had average fecundities inversely correlated with latitude. The mean age of first spawning in Atlantic salmon (Schaffer and Elson, 1975) increases with latitude and

difficulty of upstream migration. Leggett and Carscadden (1978) found that the proportion of repeat spawners increases with the latitude of the home river in shad (Alosa sapidissima). Fecundity decreases as the proportion of repeat spawners increases. If environmental predictability can be inversely correlated with latitude this result fits the theory of bet-hedging. There is some direct evidence of the effect of environmental instability on reproductive strategy. Murphy (1968) learned that Peruvian anchovies reproduce in the stable Peruvian current, mature at 1 year, reproduce for 2 years, and have a 2x factor of variation in spawning success. Conversely, Atlanta-Scandian herring which reproduce in the unpredictable polar front region, mature at 5 to 6 years, reproduce up to 18 years, and have a 25x factor of variation in spawning success (Murphy, 1968). In addition, female spotted salamanders (Ambystoma maculatum) from a permanent pond produced more and smaller eggs than females in a temporary pond (Woodward, 1982).

Environmental predictability inferred by latitude is only one of many factors correlated with variation in life histories. For example, Hubbs and Johnson (1961) found that fecundity and egg diameter of the dusky darter (Percina sciera) at Austin and San Marcos, Texas, was inversely correlated with intraspecific competition. Plaice (Pleuronectes platessa) have higher fecundities where population density is low (Bagenal, 1966). Better fed brown trout (Salmo trutta) matured earlier, grew faster, and contained significantly more and smaller eggs than starved fish (Bagenal, 1969). Trout in mountain streams lay fewer and smaller eggs than conspecifics in the lowlands (Bagenal, 1969). Terrestrial species of salamander experience greater uncertainty in abundance of prey items relative to aquatic species, and have smaller and

less frequent clutches (Jaeger, 1981).

The Environment

In spite of many correlative relationships some data support the hypothesis that variable environments can affect fish. Effects of temperature can be great at early life history stages (Hubbs et al., 1969). Eggs have definite temperature tolerance limits (Gerking, 1980). Higher temperatures can result in higher swimming speeds which may be important in thwarting predators (Wardle, 1980). A relationship has been shown between deviations in air temperature (occurring 3 years earlier than the landings) and the availability of mackerel (Taylor et al., 1957; Figure 1).

The major problem with evaluating the effect of environmental predictability has been the inability to quantify predictability on animal populations. Colwell (1974) attempted to remedy this situation by developing equations that could quantitatively describe the predictability of periodic phenomena (Appendix A). Stearns (1981) examined these equations using computer simulations and found their overall performance to be good.

Noturus exilis Nelson

There is little information on the life history of madtoms although research has been done on N. albater (Mayden et al., 1980), N. exilis (Curd, 1959; Mayden and Burr, 1981), N. gyrinus (Mahon, 1977), N. insignis (Clugston and Cooper, 1960), N. miurus (Burr and Mayden, 1982), and N. nocturnus (Orth, 1980). The study by Mayden and Burr (1981) on N. exilis qualifies as the best comprehensive study (Table II). A

Figure 1. Landings of Mackerel, 1804-1950, in New England (Solid Line)
           Compared with Annual Deviations in Air Temperatures at
           New Haven, Connecticut, Occurring 3 Years Earlier than the
           Landings. Taken from Taylor et al. (1957).

TABLE II

SUMMARY DATA ON NOTURUS EXILIS
FROM GREEN CREEK, ILLINOIS

Parameter	Data
Location	Green Creek, 7.2 km W Anna, Union Co., Illinois.
Stream Aspect	Small, Spring-fed, First Order Trib.
Stream Width	1.5-7.5 m.
Stream Depth	4 cm to 2m (Most Less Than .5 m).
Habitat Preference	Juveniles Usually in Shallow Riffles and Adults in Pools (Except in Breeding Season).
Diet	Benthic Insects: Dipteran Larvae and Pupae, Mayfly Naiads, Trichopteran Larvae, and Some Crustaceans Composed 95 per cent of the Diet.
Maximum Age	59 Months.
Age Structure	64.0% 0+, 33.3% 1+, 2.2% 2+, .5% 3+.
SL - Age Regression	$SL = 23.0 + 2.41A - 0.022A^2$
ADJWT*- SL Regression, Males	$Log_{10}ADJWT = -4.92 + 3.03Log_{10}SL$
ADJWT - SL Regression, Females	$Log_{10}ADJWT = -4.63 + 2.88Log_{10}SL$
Year of Maturity, Male	2 (Third Summer)
Year of Maturity, Female	1-2 (Size Dependent)
Fecundity - SL Regression	$F = -142.2 + 3.47SL$
F - Age Regression	$F = 6.36 + 3.45A$
F - ADJWT Regression	$F = 3.49 + 18.73ADJWT$
Time of Spawning	May to July
Sex Ratio	1.1 Female : 1.0 Male ($p < 0.05$)

TABLE II (Continued)

Parameter	Data
Nesting	In Cavity Under Rock, Board, etc.
Parental Care	By Male, Leaves After Yolk Sacs Absorbed.
Number of Eggs per Nest	Significantly Correlated with Male Size.

* Weights are adjusted body weights (ADJWT = total weight minus viscera).

Source: Mayden and Burr (1981).

food habits study on N. exilis from northeastern Oklahoma revealed

similar dietary preferences (Curd, 1959).

CHAPTER III

DESCRIPTION OF STUDY AREAS

Samples for this study were taken from two streams, Flint Creek and Cloud Creek, located in the Ozark biotic district (Blair and Hubbell, 1938). The Ozark biotic district is characterized by the presence of Boone Chert from the Mississippian period. Study sites at both creeks have gravel banks and forested edges, or are lined by limestone outcrops. Both creeks are inhabited by characteristic Ozarkian fish assemblages (Miller and Robison, 1973; Appendix B).

Flint Creek is a springfed, third order tributary of the Illinois River located in Delaware County, Oklahoma. My study sites were located in R 25 E, T 20 N, Sec 14, 24, and 25. Flint Creek has a substrate of gravel, cobble and rubble and is characterized by a swift current. Width ranges from 5 m to 30 m. Depths range from .2 m to 2 m but typically are less than .5 m.

Cloud Creek is a first order stream also in Delaware County. My study site was located in R 24 E, T 21 N, Sec 29, approximately 8 km north of the Flint Creek study site. This stream is a tributary of Spavinaw Creek wich feeds into the Grand River. The bottom is composed of gravel, cobble, and rubble. Width ranges from 1.5 m to 5 m and depth ranges from .2 m to 1.5 m.

CHAPTER IV

METHODS AND MATERIALS

Data on N. exilis from Flint Creek were compared with similar data

taken from Green Creek. by Mayden and Burr (1981). I made one collection

from Cloud Creek during the 1982 spawning season to determine extent of

variability between two sites in similar areas but different drainages.

Specimens of N. exilis were collected approximately monthly from

13 February 1981 to 23 May 1982 (Table III). Madtoms were collected by

kicking substrate in front of a stationary 2 m common sense seine.

Specimens were placed in 10 per cent formalin for 3 days, washed in

water for 3 days, and finally placed in 40 per cent isopropyl alcohol.

Habitat use was quantified at each sampling time from 13 February

1981 to 5 January 1982. A numbered cork, attached to a weight, was

placed at each spot where one or more madtoms were taken. Habitat

measurements and observations were then made at each marked location.

Depths and currents were determined with a Gurley Pygmy Current Meter.

Substrate, in an area 1 m around the cork, was qualitatively categorized

as silt, gravel, cobble, or rubble or combinations of these. Silt is

defined as substrates up to 1 mm in size, gravel from 1 to 64 mm, cobble

from 64 to 256 mm, and rubble greater than 256 mm (modified from Hynes,

1970).

Lengths used are standard lengths (SL). Total weights (WT) were

used unless indicated otherwise. Adjusted body weight (ADJWT: total

TABLE III

COLLECTION DATES AND NUMBER
OF <u>N</u>. <u>EXILIS</u> CAPTURED

Site	Date	Number Captured	
		Males	Females
Flint Creek	2/13/81	5	7
	3/08/81	7	4
	3/28/81	3	5
	4/25/81	8	7
	5/24/81	5	5
	6/21/81	-	2
	7/18/81	-	-
	8/15/81	-	1
	9/13/81	2	1
	10/11/81	-	4
	11/07/81	2	1
	12/05/81	2	2
	1/05/82	-	3
	2/27/82	4	1
	3/13/82	10	8
	4/03/82	17	19
	4/10/82	18	13
	5/14/82	21	15
	5/23/82	-	1
Cloud Creek	5/23/82	11	24

weight minus stomach, air bladder, kidney, and gonads) was used for fish collected 14 May 1982 and 23 May 1982, to provide comparative data for that of Mayden and Burr (1981).

Stomachs from fish taken 13 February 1981 to 28 March 1981, were excised at the esophagus and separated from the intestine at the pyloric valve. Prey items were identified to the lowest practical taxon.

The fourth or fifth vertebra was removed for aging. Vertebrae were dried, cleaned, and examined at 20 to 40 power against a dark background with a dissecting microscope. The number of annuli were counted and used in age and growth determinations (Hooper, 1949; Gilbert, 1953; Carlson, 1966; Mahon, 1977). One hundred and fifteen madtoms collected from 19 August 1946 to 25 August 1946 in the Illinois River drainage by George Moore et al. (Oklahoma State University Museum Catalog No. 2502, 2536, 2542, 2565, and 2664) were measured for length frequency data.

Gonads were removed and weighed to 4 decimal places. Ovary and testis weight was divided by total weight minus stomach weight and gonad weight to determine the gonosomatic index (GSI). Mature eggs were counted and an average diameter determined from at least 10 eggs. Egg diameters were measured with an ocular micrometer.

Methods for using Colwell's equations are outlined in Appendix A. Predictability estimates were generated with 10 year summary data for air temperature and rainfall (NOAA Climatic Data; Appendix C). Water temperatures and flow estimates were taken from 13 February 1981 to 5 January 1982 and correlated with air temperature and rainfall respectively to establish the relative importance of the variables entered into Colwell's equations. To estimate discharge, current speed and depth were taken at 1 m intervals on a transect across Flint Creek. The

average current and depth could then be estimated for each meter interval of water. These estimates were summed to get a discharge estimate for that date.

Data were analyzed in part with the Statistical Analysis System (SAS). Other methods and tests followed methods of Sokal and Rohlf (1969) and employed statistical tables from Snedecor and Cochran (1980). If not specified a significance level of $\alpha = 0.05$ was used.

CHAPTER V

RESULTS

Environmental Predictability

Two major factors, flow and temperature, affect fish in streams.
These factors are both estimated by air temperatures and precipitation
data. To relate these variables to the aquatic environment, air temp-
eratures were correlated with water temperatures taken at Flint Creek.
Rainfall totals from a 10 day period before sampling were also cor-
related with flow estimates. Water temperatures are significantly cor-
related with monthly temperature means (Figure 2). A trend, although
nonsignificant at the 0.05 level, shows flow to increase with increas-
ing rainfall (Figure 3).

Predictability estimates were made for several locations of differ-
ing latitudes (Table IV; see Appendix C for raw data). Predictability
of air temperatures is inversely correlated with latitude (Figure 4).
No clear pattern emerges, however, for predictability of rainfall
(Figure 5). Cairo, which is near Green Creek, is less predictable in
air temperature but more predictable in amount of rainfall than Tulsa
which is near Flint Creek and Cloud Creek.

Colwell's equations result in a predictability estimate over 12
months for 10 years. Computing the coefficient of variation (C.V.) for
deviations from the mean for each month over 10 years allows an estimate

Figure 2. Water Temperatures at Collection Dates versus Monthly Air
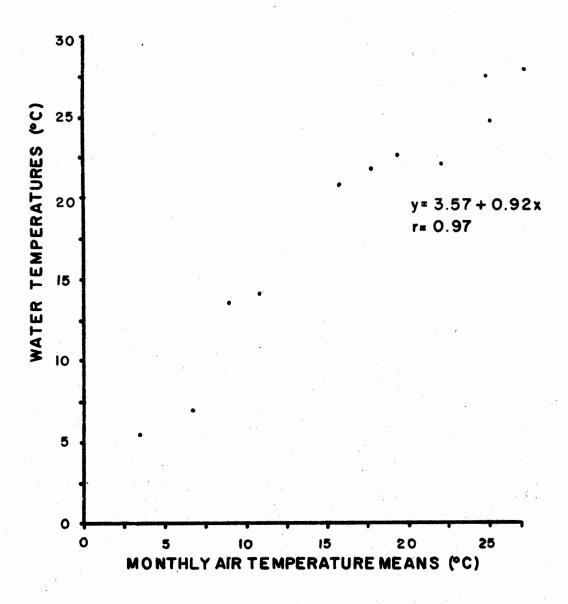   Temperature Means.

Figure 3. Flow Estimates for Collection Dates versus Total Precipitation 10 Days Prior to the Collection Dates.
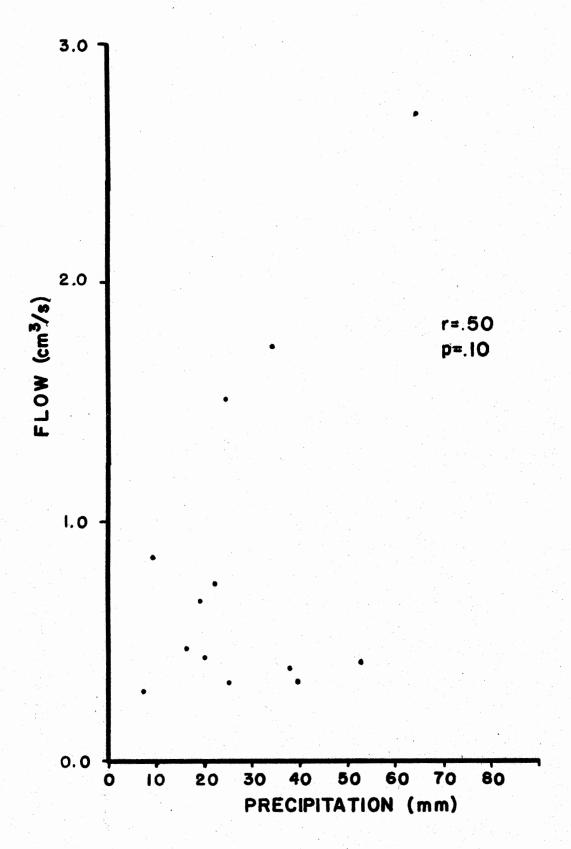
TABLE IV

PREDICTABILITY ESTIMATES USING 10 YEARS
(1970-1979) OF SUMMARY DATA

Location	Latitude (Hundreths)	Predictability of Air Temperatures	Predictability of Rainfall
Lake Charles, LA	30.25	.81	.37
Shreveport, LA	32.50	.78	.46
Tulsa, OK	36.13	.75	.40
Cairo, IL	36.98	.72	.44
Peoria, IL	40.75	.72	.42
Madison, WI	43.08	.70	.51

Figure 4. Predictability Estimates for Air Temperature Using Colwell's
(1974) Equations Plotted Against Latitude. Each Point
Represents the Geographical Location for Which Climatic
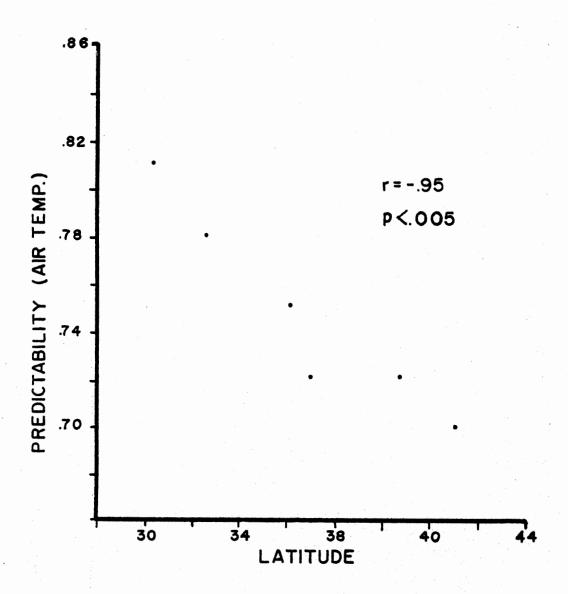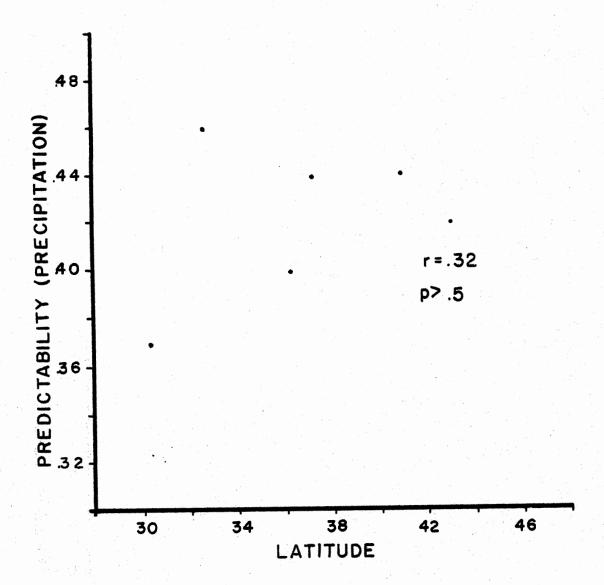Data was Used in the Equations.

Figure 5. Predictability Estimates for Precipitation Using Colwell's
(1974) Equations Plotted Against Latitude. Each Point
Represents the Geographical Location for Which Climatic
Data was Used in the Equations.

Figure showing scatter plot of PREDICTABILITY (PRECIPITATION) versus LATITUDE with r = .32, p > .5

of variability for each month (modification of procedure from Horowitz, 1978). Using this method allows monthly variability to be compared to different life history stages for the two sites (Figures 6 and 7).

Comparative Life Histories

Habitat

Flow over a 1 year period in Flint Creek peaked in the spring and fall (Figure 8). Temperatures for the sampling period are shown in Figure 9. Flint Creek does not freeze over completely, but freezing may occur over pools and edges away from the main channel. Water temperature of Flint Creek tracks the air temperature closely (Figure 2).

N. exilis in Flint Creek prefer moderate currents (Figure 10, $\bar{x}$ = 38 cm/s), shallow depths (Figure 11, $\bar{x}$ = 18 cm), and a variety of substrates (Figure 12). N. exilis were associated most often with gravel riffles under a larger stone (Figure 13). This association with large rocks, may provide shelter and protection from predators (Taylor, 1969).

Diet

Diet analysis (N = 37) resulted in data similar to those of previous studies (Curd, 1959; Mayden and Burr, 1981). Madtoms in Flint Creek consume ephemeropteran naiads and dipteran larvae and pupae most frequently by number (Table V). These taxa also occurred in proportionally more stomachs. Nine stomachs were empty but because fish were collected in the late afternoon, some food must be eaten during the daylight hours.

Figure 6. Coefficients of Variation for Deviations from Air Tempera-
          ture Means Plotted Against Month. Each C.V. was Computed
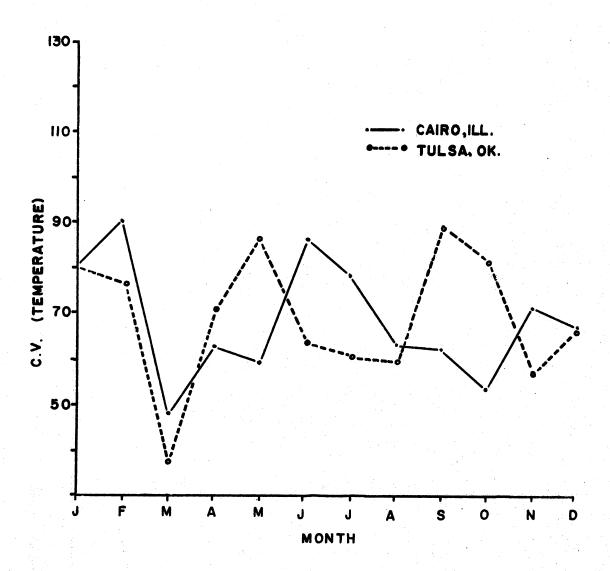   from 10 Years Data for each Month.

Figure 7. Coefficients of Variation for Deviations from Precipitation
          Means Plotted Against Month. Each C.V. was Computed from
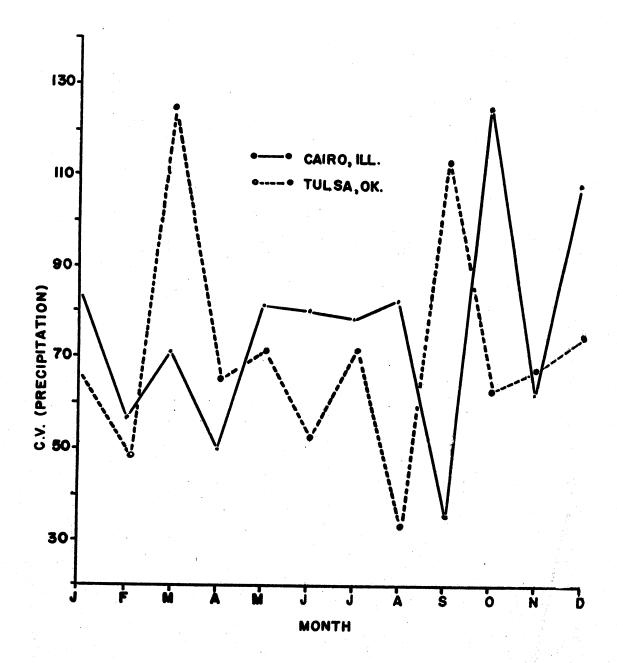   10 Years Data for each Month.
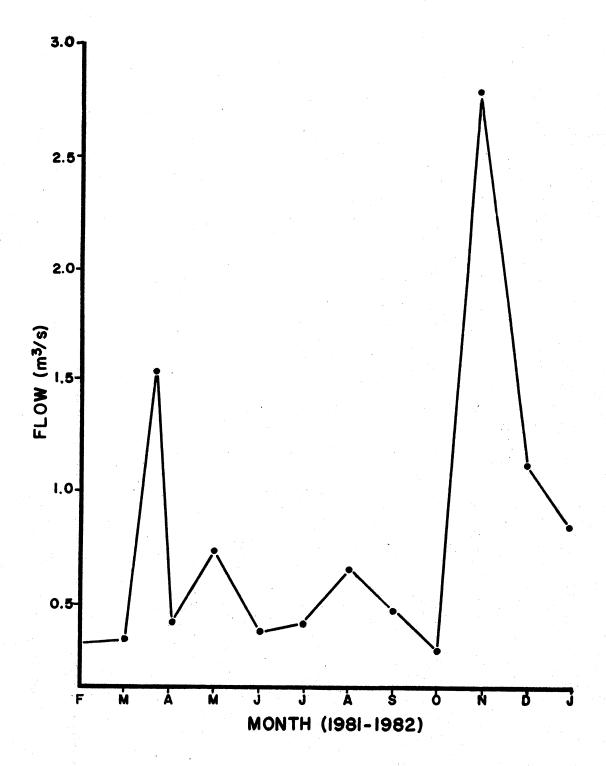
Figure 8. Estimates of Flow in Flint Creek versus Time.
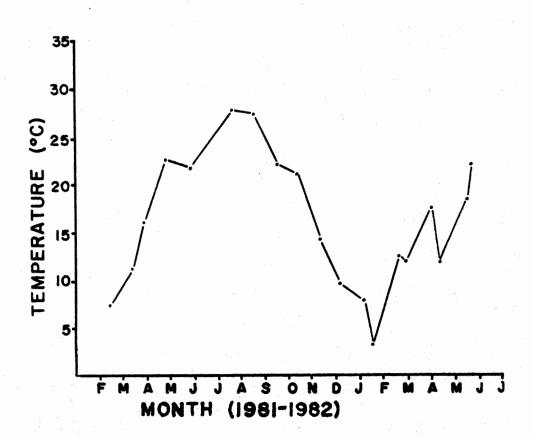
Figure 9. Water Temperature in Flint Creek versus Time.

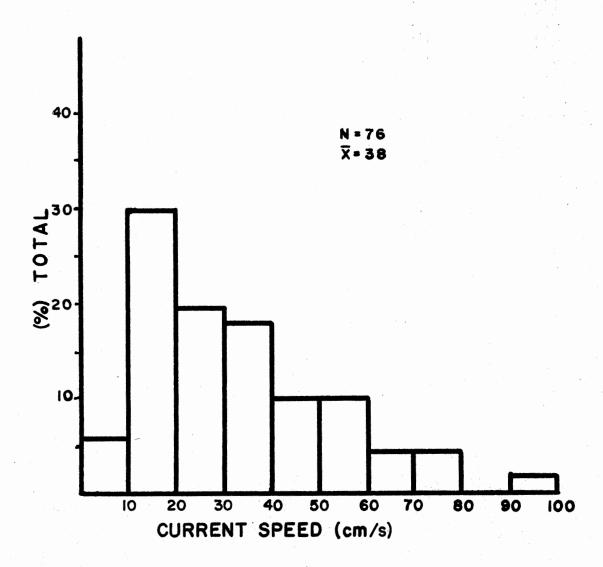Figure 10. Percentage of N. exilis Captured at each 10 cm/s Category
of Current Speed.

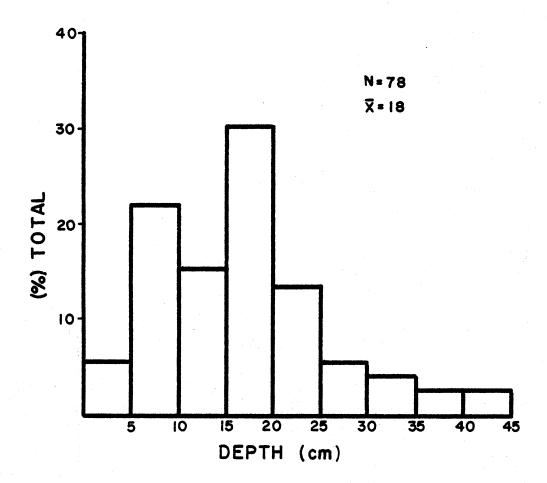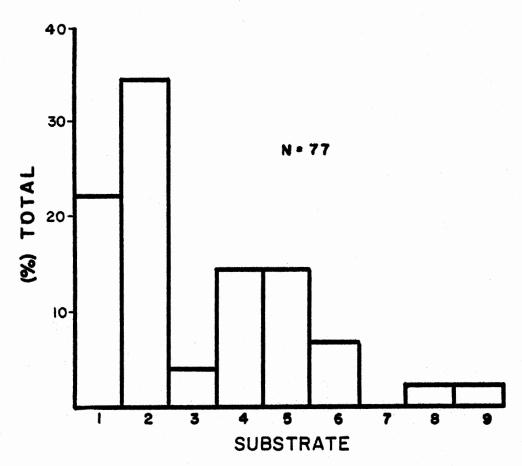Figure 11. Percentage of N. exilis Captured at each 5 cm Category of
        Depth.

Figure 12. Percentage of N. exilis Taken at Different Grades of
            Substrate.

1. GRAVEL
2. GRAVEL-COBBLE
3. GRAVEL-RUBBLE
4. COBBLE-GRAVEL
5. COBBLE

6. COBBLE-RUBBLE
7. RUBBLE-GRAVEL
8. RUBBLE-COBBLE
9. RUBBLE

Figure 13. Percentage of <u>N. exilis</u> Taken at Different Categories of
Habitat Classification.

N = 66

(%) TOTAL

STREAM ASPECT

1. ABOVE RIFFLE
2. RIFFLE
3. RACEWAY
4. BELOW RIFFLE
5. RIFFLE EDGE
6. POOL

TABLE V

DIET ANALYSIS OF <u>N</u>. <u>EXILIS</u>

Taxon	Frequency of Occurrence in Stomachs	Per Cent of Total Number of Items
Insecta		
Plecoptera		
Perlidae		
<u>Phasganophora</u> sp.	8.7 (%)	1.4 (%)
<u>Acroneuria</u> sp.	8.7	1.4
Perlodidae		
<u>Isogenus</u> sp.	4.3	0.7
Ephemeroptera		
Baetidae		
<u>Ephemerella</u> sp.	26.1	18.4
<u>Leptophlebia</u> sp.	34.8	12.5
<u>Centroptilium</u> sp.	17.4	4.4
<u>Baetis</u> sp.	4.3	0.7
<u>Isonychia</u> sp.	8.7	1.5
Heptageniidae		
<u>Stenonema</u> sp.	26.1	5.9
Trichoptera	4.3	0.7
Lepidoptera	13.0	2.9
Diptera		
Chironomidae		
Larvae	82.6	47.0
Pupae	26.1	5.1
Hirudinea	8.7	1.5
Pebbles	17.4	----
Unidentified Materials	82.6	----

Age and Growth

Length frequency data on 115 fish collected over a 6 day period in 1946 did not allow identification of different age classes (Figure 14). However, vertebral analysis revealed opaque rings representing fast growth and translucent narrow rings representing slow growth. The narrow rings appeared to be laid down in April, prior to spawning. Mayden and Burr (1981) showed similar results with N. exilis. Mahon (1977) showed that aging fish with vertebrae verified length frequency age determination but my data did not support this conclusion. Some fish are difficult to age because of the formation of checks or accessory rings. Gilbert (1953) found that these checks are usually incomplete whereas true annuli were always complete. I found that checks were usually found before the first annulus and were not as deeply indented into the vertebra as true annuli. Because May and early June coincided with peak spawning activity June was designated month one in the analysis.

The oldest individual captured was a 48 month old male, 70.0 mm SL and 6.67 g total body weight. Most fish were of the 0+, 1+, and 2+ year classes (Figure 15). Individuals from 0 to 11 months are 0+, from 12 to 23 months are 1+, etc. Sampling error probably was responsible for the low number of 0+ class fish taken. N. exilis from Flint Creek and Green Creek have significantly (Chi-square, p<.005) different age class frequencies (Table II, Figure 15). Flint Creek has a larger proportion of 2+ and 3+ fish. This result is potentially biased by different collecting techniques.

I collected no 0+ fish in July or August of 1981, so I have

Figure 14. Length Frequency Data for N. exilis Collected in August 1946
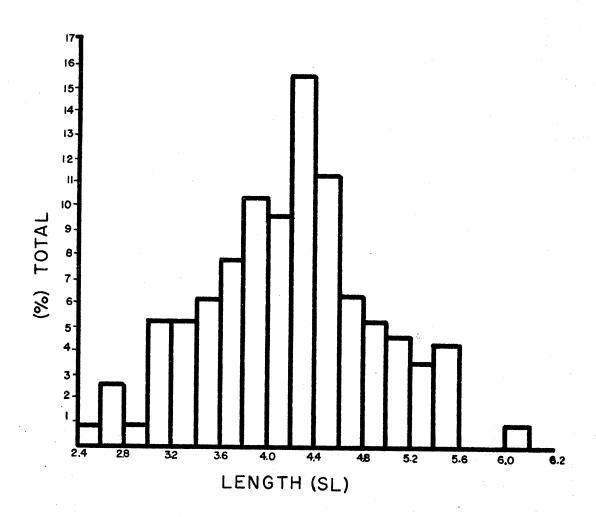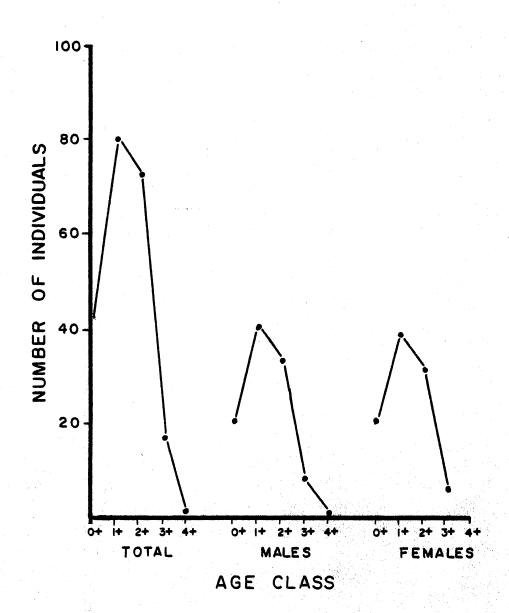   by George Moore et al. from the Illinois River Drainage.

Figure 15. Age Class Frequency Distribution of <u>N</u>. <u>exilis</u> from Flint
          Creek.

included lengths and weights from nine fish collected 21 August 1946
(Okla. State Univ. Museum Catalog No. 2538) from the Illinois River.
Weight increased with length curvilinearily (Figure 16). The weight
versus standard length equation for males and females is $\log_{10}WT =$
$-4.971 + 3.1241\log_{10}SL$ ($r = .97$, $N = 110$) and $\log_{10}WT = -4.63 + 2.926$
$\log_{10}SL$ ($r = .84$, $N = 104$) respectively. Males and females increase in
weight at the same rate per unit increase SL ($t_s = 1.46$, $p > .05$). The
intercepts are significantly different ($t_s = 26.41$, $p < .001$) showing
males to be of greater weight at the same standard length than females.
Male N. exilis are also significantly heavier per unit standard length
than females in Green Creek (Mayden and Burr, 1981).

Mayden and Burr (1981) used adjusted body weight, so a direct com-
parison could not be made with most of my data. However, adjusted body
weights were taken on 35 fish collected 14 May 1982 and the equation
$\log_{10}ADJWT = -4.88 + 3.06\log_{10}SL$ ($r = .97$) was calculated. Significance
testing against the Green Creek population was not possible since the
regression and residual sum of squares was not given in Mayden and
Burr (1981). Visual inspection indicates Flint Creek madtoms reach
greater weights per unit length than madtoms from Green Creek (Figure
17). For example by using the calculated equations a madtom 65.0 mm SL
would be predicted to weigh 4.65 g ADJWT in Flint Creek and 3.63 g ADJWT
in Green Creek.

The curvilinear equation describing standard length and age was
$SL = 24.68 + 2.015A - 0.020A^2$ (Figure 18). Log transformed equations
$\log_{10}SL = 1.300 + 0.3421\log_{10}A$ ($r = .84$) for males and $\log_{10}SL = 1.293 +$
$0.3481\log_{10}A$ ($r = .84$) for females were not significantly different ($t_s =$
$.33$, $p > .50$). No differences between sexes was found in this relationship

Figure 16.   Total Body Weight of N̲. exilis Plotted Against Standard
            Length.

$LOG_{10}WT = -4.79 + 3.02 \ SL$

$r = .91, \ N = 214$

Figure 17. Relationship of Body Weight and Standard Length for N. exilis
            Data Logrithmically Transformed.

FLINT CREEK —
LOG_{10} ADJ.WT = $-4.88 + 3.06$ LOG_{10} SL
$r = .97$, $N = 35$

GREEN CREEK ----
LOG_{10} ADJ.WT = $-4.77 + 2.94$ LOG_{10} SL
$r = .98$, $N = 241$

LOG_{10} ADJUSTED BODY WEIGHT

LOG_{10} SL

Figure 18. Regression of Standard Length on Age for <u>N</u>. <u>exilis</u>.

$SL = 24.68 + 2.015A - 0.020A^2$

$r = .96$

for Green Creek madtoms (Mayden and Burr, 1981). In addition, no sig-
nificant differences were distinguished between equations describing
Green Creek and Flint Creek N. exilis.

Condition factors (K), an index of relative plumpness (Bagenal,
1978), were computed for each fish, a monthly average taken and plotted
against time (Figure 19). The months of July through March have the
lowest averages while K factors from April to June (spawning season) are
highest. This seasonal pattern results in part from females putting on
ovarian weight, and males putting on enlarged cephalic muscles due to
nest building (Mayden and Burr, 1981).

Reproduction

Spawning Season. Spawning season was determined by plotting the
mean gonosomatic index and mean ova diameter for each collection against
time (Figures 20 and 21). High reproductive condition in Flint Creek
madtoms occurred from late April to the end of June. Maximum gono-
somatic index and ova diameter values occurred during the last 2 weeks
of May and the first two weeks of June in 1981 and 1982. However,
extended or multiple spawning may occur since one fish (Okla. State
Univ. Museum Catalog No. 2538) taken on 21 August 1946, contained 52
mature ova.

Reproduction of Females. Thirteen 12 month old females were exam-
ined for reproductive condition (Table VI). Females with mature or
maturing ova had an average weight of 1.77 g and an average length of
47.4 mm SL. Mayden and Burr (1981) found 35 of 169, 12 month old
females to be possible spawners.

Figure 19. Condition Factors $(K = 100WT/SL^3)$ versus Time.

Figure showing K FACTOR (IOOWT/SL^3) versus MONTH (1981-1982)
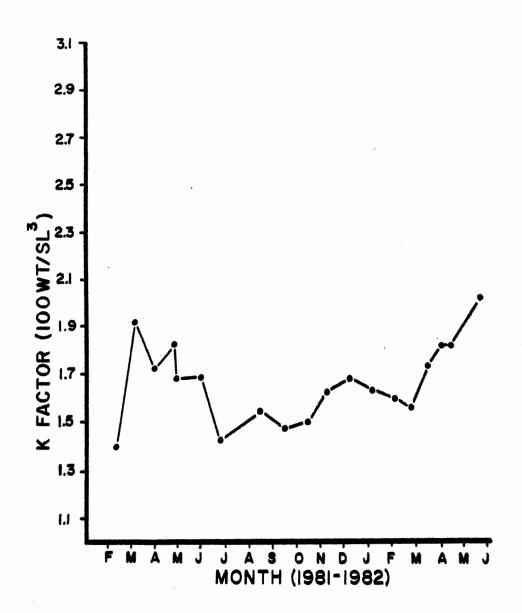
Figure 20. Gonosomatic Indices (Gonad Weight x 1000 / Total Body Weight
         Minus Gonad Weight and Stomach Weight) versus Time.
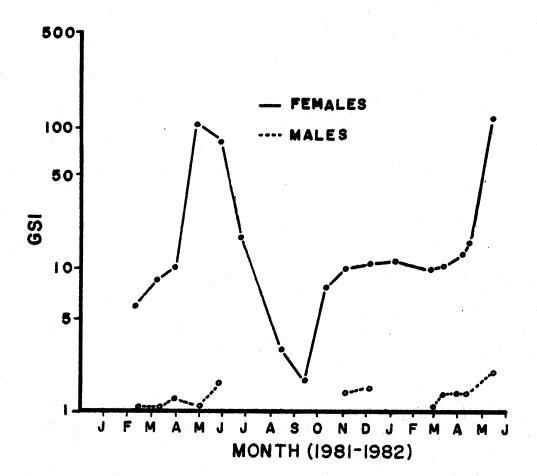   Vertical Scale is Logarithmic.

Figure 21. Mean Ova Diameter for All Fish Collected During a Sampling
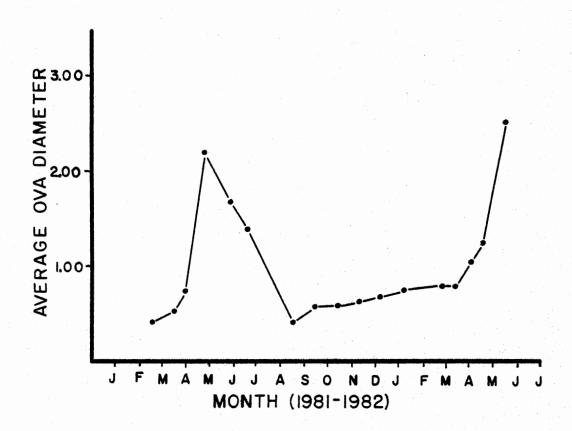   Trip. At Least 10 Ova per Fish were Measured.

TABLE VI

DATA ON 0+ AGE CLASS FEMALES TAKEN
FROM FLINT CREEK AND CLOUD CREEK

Potential Spawners			Non-Spawners		
ADJWT	SL	K	ADJWT	SL	K
2.18	47.8	1.996	0.93	44.8	1.223
1.78	48.0	1.610	0.65	33.6	2.030
1.68	47.6	1.558	1.58	44.0	1.855
1.29	43.6	1.556	1.78	46.6	1.759
2.39	52.1	1.690	1.26	41.6	1.750
1.31	45.6	1.382	1.16	43.1	1.449
1.75	47.1	1.675			
$\bar{x}$ = 1.77	47.4	1.638	1.23	42.3	1.678

Raw data used for analysis of reproductive characteristics are given in Appendix D.

Though fish from Green Creek apparently have more ova per gram adjusted body weight than fish from Flint Creek and Cloud Creek, Oklahoma females used in this comparison all weighed less than 5.0 g (Figure 22). In contrast, Mayden and Burr (1981) were able to include some of the larger females in the population. The most effective test comparing fecundities from the 3 populations would be to standardize reproductive effort per fish. However, several problems must be overcome in this approach.

A problem arises when estimating egg counts from preserved ovaries. At what point prior to spawning will ova that appear to be maturing give reliable counts? This problem is highlighted by Vladykov (1956) who has shown that as ova mature and diameter increases, the number of mature ova decreases (some regress). To see whether this factor operated with N. exilis, ova estimates (number of ova divided by ADJWT) were made for females captured in March, April, and May in Flint Creek. A one-way analysis of variance using months as classes (Table VII) resulted in significantly (Student-Newman-Keuls multiple range test) different estimates for each month.

To further investigate this effect I attempted to determine if accurate counts could be made once ova had reached a given size. Sample variances of ova per g ADJWT were computed for fish with ova diameters of .40 mm and greater, .50 mm and greater, up to 2.20 mm and greater. These variances were plotted against the minimum ova size diameter used in the calculations of sample variance (Figure 23). Variance leveled off at an ova diameter of 1.20 mm. For N. exilis this represents the

Figure 22. Regressions of Number of Mature Ova on Adjusted Body Weight
For Flint Creek, Cloud Creek, and Green Creek N. exilis.

GREEN CREEK
F = 3.50 + 18.73 ADJWT
r = .92, p < .001

CLOUD CREEK
F = 12.19 + 9.30 ADJWT
r = .65, p < .01

FLINT CREEK
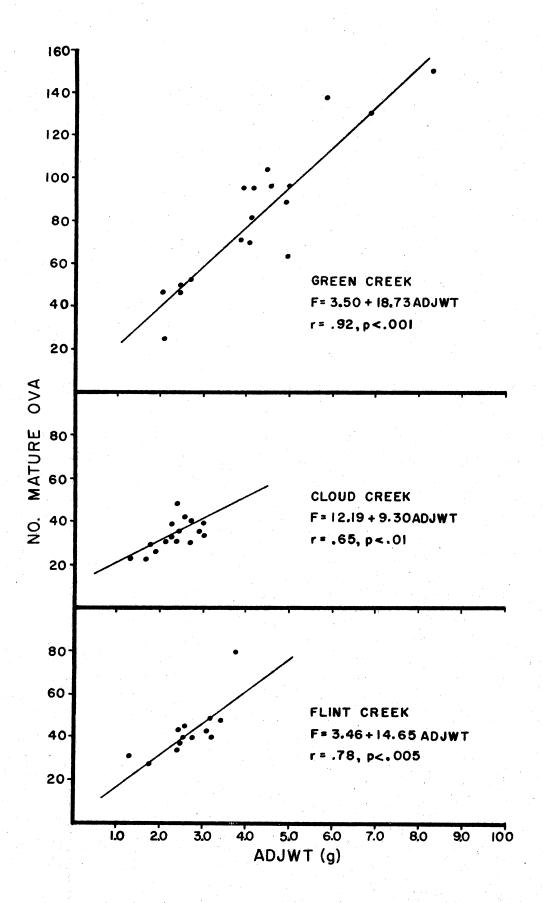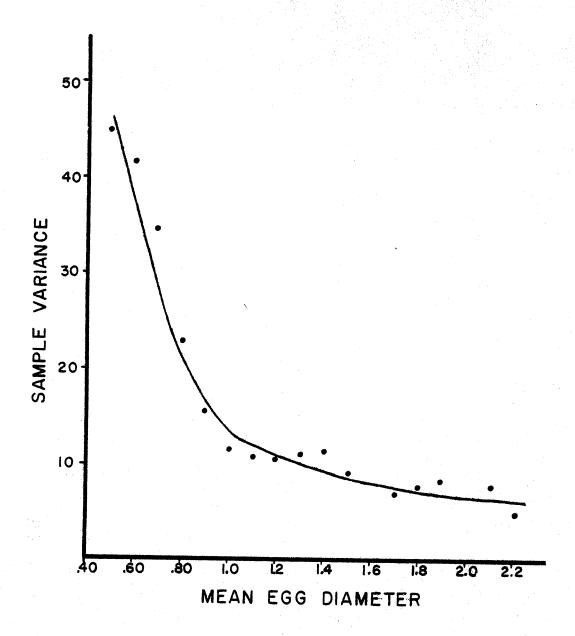F = 3.46 + 14.65 ADJWT
r = .78, p < .005

NO. MATURE OVA

ADJWT (g)

TABLE VII

ONE-WAY AOV TABLE COMPARING EGG ESTIMATES
(NUMBER OF OVA PER GRAM ADJUSTED BODY
WEIGHT) FOR MARCH, APRIL, AND MAY
IN FLINT CREEK DURING 1982

Source	d.f.	S.S.	M.S.	F	P-value
Among Groups	2	907.104	453.55	24.73	p<.001
Within Groups	50	916.941	18.34		
Total	52	1824.045			

Figure 23. Sample Variances of Ova per Gram Adjusted Weight versus
            Average Ova Diameters in Different Individuals.

upper limit for size of resting ova.

A second problem in computing reproductive effort relates to the method of standardization. Many workers relate fecundities to standard lengths. One possibility is to convert fecundities to ova per mm standard length. Since volume increases approximately as the cube of the length, this index will increase with standard length (Figure 24) and is therefore not useful unless populations of the same age and size structure are compared.

Ova per gram body weight (or ADJWT) seems to be a better index of reproductive effort since no built in bias exists with this index (Figure 25) as would be true for ova per unit age (much variability in length, weight, and fecundity exists at a specific age). Ova per gram adjusted body weight is therefore used in the reproductive comparisons that follow.

An analysis of variance was used to compare ova per g ADJWT among fish from the three sites (Table VIII). The analysis shows that fish from Flint Creek and Cloud Creek have significantly lower means that those from Green Creek but are not different from each other (Student-Newman-Keuls multiple range test). Fish from Flint Creek and Cloud Creek have larger ova than fish from Green Creek (Table IX; Student-Newman-Keuls multiple range test). To test whether there is an equal tradeoff between size and number, gonosomatic indices were compared among fish from the three sites. No significant differences exist among the three populations (Table X). However, the test is completely accurate if we compare populations at the same point in maturation, and this could not be controlled.

Even though females in the three populations are investing the same

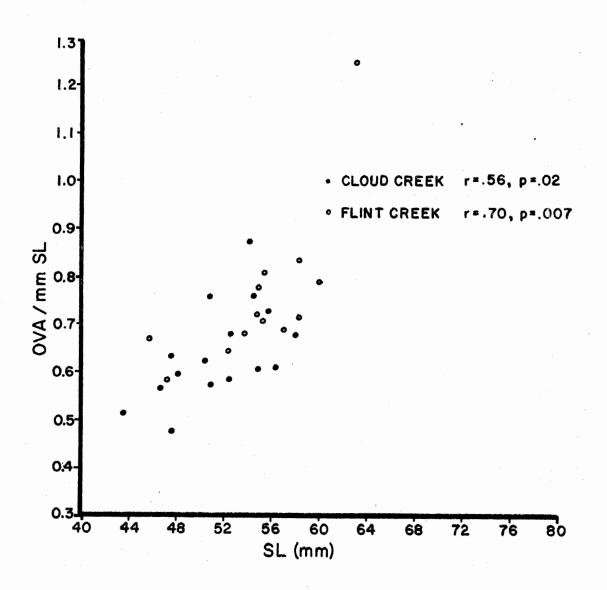Figure 24. Number of Ova per mm Standard Length versus Standard Length.

Figure 25. Number of Ova per Gram Adjusted Body Weight versus Adjust-
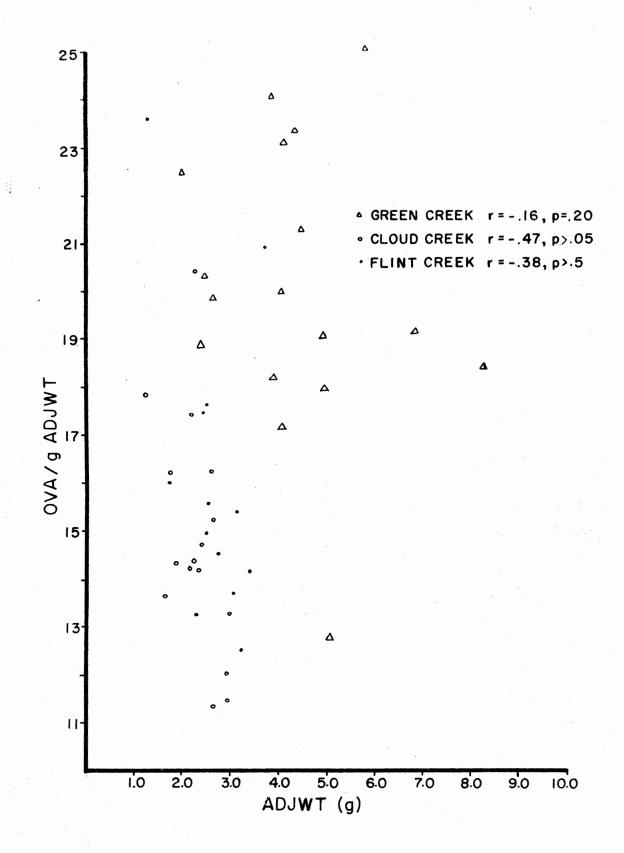ed Body Weight.

TABLE VIII

ONE-WAY AOV TABLE COMPARING EGG ESTIMATES
(NUMBER OF OVA PER GRAM ADJUSTED BODY
WEIGHT) FOR MATURE FEMALES IN THE
THREE POPULATIONS

Source	d.f.	S.S.	M.S.	F	P-value
Among Groups	2	214.016	107.01	11.53	p<.005
Within Groups	44	408.282	9.28		
Total	46	622.298			

TABLE IX

ONE-WAY AOV TABLE COMPARING OVA DIAMETERS FROM
FLINT CREEK, CLOUD CREEK, AND GREEN CREEK

Source	d.f.	S.S.	M.S.	F	P-value
Among Groups	2	1.966	.983	3.773	p<.05
Within Groups	45	11.724	.260		
Total	47	13.690			

TABLE X

ONE-WAY AOV TABLE COMPARING GONOSOMATIC INDICES
FOR FLINT CREEK, CLOUD CREEK, AND GREEN CREEK

Source	d.f.	S.S.	M.S.	F	P-value
Among Groups	2	14214.7	7107.35	1.16	p>.2
Within Groups	44	270541.0	6148.66		
Total	46	284755.7			

TABLE XI

ONE-WAY AOV TABLE COMPARING K FACTORS FOR FLINT
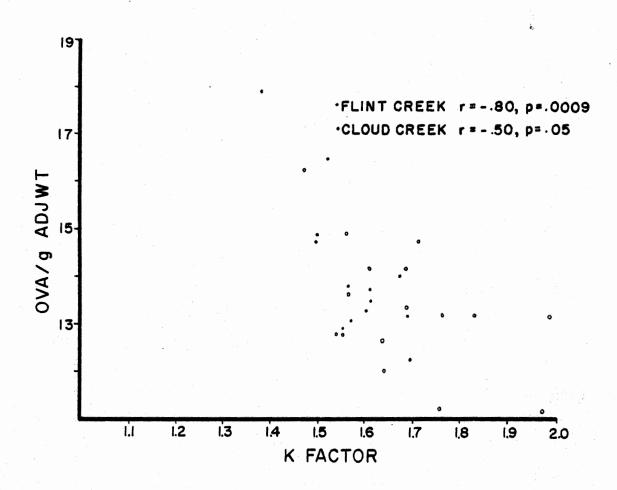CREEK, CLOUD CREEK, AND GREEN CREEK

Source	d.f.	S.S.	M.S.	F	P-value
Among Groups	2	.302	.151	9.506	p<.001
Within Groups	44	.699	.016		
Total	46	1.001			

proportional amount into reproduction, a different cost may be involved. This cost may be measured by comparing differences in K factors among the three populations. Cloud Creek has the largest average K followed by Flint Creek and finally Green Creek (Table XI). All differences were significant (Student-Newman-Keuls multiple range test).

Negative correlations exist between ova per gram adjusted body weight and condition in Flint Creek and Cloud Creek ($r = -.80$, $p = .0009$; $r = -.50$, $p = .05$, respectively) but this relationship is not seen in the Green Creek population ($r = .10$, $p = .70$). For Flint Creek and Cloud Creek an increase in reproductive effort reduces somatic condition (Figure 26). Absence of correlation in the Green Creek population indicates a fixed cost for the current reproductive effort.

Nesting. One egg cluster was dislodged during seining 23 May 1982 at Cloud Creek. Water temperature was $22^{\circ}C$. The cluster contained 44 eggs with an average diameter of 4.47 mm (range 3.8 to 4.9 mm, S.D. = .259). Mayden and Burr (1981) found eggs in a cluster averaged 4.11 mm in diameter. Eggs were light yellow in color. Most madtoms collected during the spawning season were aggregated, with large numbers occurring in a small area. Perhaps an olfactory signal is employed in mate attraction as in other ictalurids (Todd, 1971).

Figure 26. Regression of Ova per Gram Adjusted Body Weight on Con-
dition Factor (K).

CHAPTER VI

DISCUSSION

Some life history variation existed among geographically separated
populations of N. exilis (Table XII). However, no differences existed
between Flint Creek N. exilis and Cloud Creek N. exilis fecundities and
ova diameters. These populations are separated geographically by
approximately 8 km, but empty into different drainages (separated by 280
river km and 6 dams). Isolated populations, in close proximity to each
other, have been shown to have similar life histories. This result is
expected if regional climatic or environmental influences shape life
history characteristics by natural selection. Such results would seem
to support the initial assumption upon which this study was based. The
possibility cannot be discounted, however, that recency of isolation and/
or gene flow explains the similarity of Flint Creek and Cloud Creek pop-
ulations. In contrast, Green Creek N. exilis did show differences in
life history characteristics from the Flint Creek and Cloud Creek pop-
ulations.

Flint Creek and Cloud Creek madtoms tend toward the set of char-
acteristics historically associated with K-selection, while Green Creek
madtoms tend toward those associated with r-selection. Flint Creek and
Cloud Creek N. exilis best fit the r- and K-selection model when compar-
ed to Green Creek N. exilis if their environment is more stable than
that of Green Creek. Colwell's equations show Tulsa to have more

TABLE XII

SUMMARY OF FLINT CREEK, CLOUD CREEK, AND GREEN CREEK
LIFE HISTORY SIMILARITIES AND DIFFERENCES

Characteristic	Data Summary
Habitat	Similar; but Flint Creek N. exilis occupy riffles more frequently.
Diet	Similar.
Maximum Age	Green Creek N. exilis 59 months, and Flint Creek N. exilis 48 months.
Age Structure	Flint Creek contains more fish in 2+ and 3+ year classes.
Year of Maturity (Male)	1 to 2 years depending on size.
Year of Maturity (Female)	1 to 2 years depending on size.
Growth	Flint Creek fish reach greater weight per unit SL. Flint Creek and Green Creek madtoms have similar SL and Age equations.
Reproductive Effort	Same amount of ovarian weight invested in proportionally.
Ova Number per g ADJWT	Green Creek > Flint Creek = Cloud Creek.
Size of Ova	Cloud Creek = Flint Creek > Green Creek.
Spawning Season	Extends from April to July in both locations.
Degree of Iteroparity	Flint Creek > Green Creek (Conclusion based on age structure).

predictable yearly air temperatures but less predictable yearly rainfall (Figures 4 and 5). However, variability is higher in Cairo in both variables during May, June, and July (the peak spawning months; Figures 6 and 7).

Alternate hypotheses may also explain this pattern. (1) If populations are at carrying capacity in Flint Creek and Cloud Creek, theory predicts that these populations should be more K-selected (MacArthur and Wilson, 1967) than the Green Creek population. (2) Perhaps larger eggs and, presumably, hatchlings of N. exilis in Flint Creek and Cloud Creek are evolutionarily constructed to escape certain egg predators not encountered (or less common) in Green Creek. A situation of this type has been found in populations of Poecilia reticulata in Trinidad (Reznick and Endler, 1982). Perhaps environmental variability, density, and survivorship may all shape the life history of N. exilis.

However, in order to fully discredit the bet-hedging model, mortality rates of adults, juveniles, and eggs at the various sites must be collected. Survivorship data are difficult to obtain over a large geographic area. Adequate density estimates are also difficult to obtain because of sampling problems (e.g. contagious distributions, distributions that change seasonally). In addition, fish densities must be related to carrying capacity in determining whether one population should be more r- or K-selected than another. It is apparent that only in laboratory or artificial stream channel experimentation where variables can be controlled, will these questions be satisfactorily answered. Small fishes with short generation times (Gambusia affinis, Brachydanio rerio)would be the most effective study organisms (Stearns, 1976b, 1977).

In the temperate zone little predictability (constancy) exists from

month to month but varying amounts may exist from season to season. These seasonal predictabilities are most important to fish passing through various life history stages. Climatic data should be analyzed for longer time spans over larger geographic areas to identify patterns (e.g. by latitude, longitude, or altitude). These patterns would then be available for use in interpretation of comparative life history results.

For aquatic systems, water temperature and rainfall are important variables. In a stable, spring-fed stream the effects of rainfall might be less important than the effects of temperature or vice versa in an intermittent stream. Variables of this type can be weighted correctly only if tied to the survivorship of the fish.

The strength of comparative studies is in repetition of observed patterns. If patterns, such as shown in this study, can be repeatedly verified and associated with a factor such as environmental predictability or density, causation may be implied. A thorough literature review on species with a large data base (e.g. salmon, R.J. Miller---in preparation) can reveal evolutionary patterns in the development of a life history strategy. Although comparative studies do not offer direct verification of the underlying mechanism controlling life histories, certainly models may be developed that give good predictions of expected life history characteristics in a given situation.

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APPENDIXES

APPENDIX A

COLWELL'S EQUATIONS

This material is extracted from Colwell (1974). For more detailed information refer to the paper. A frequency matrix is set up with 't' columns (times within a cycle) and 's' rows (states of the phenomena). Let N_{ij} be the number of cycles for which the phenomenon was in state 'i' at time 'j'. Column totals (X_j), row totals (Y_i), and the grand total (Z) are defined as

$$X_j = \sum_{i=1}^{s} N_{ij} \; ,$$

$$Y_i = \sum_{j=1}^{s} N_{ij} \; ,$$

and

$$Z = \sum_i \sum_j N_{ij} \; .$$

The uncertainty with respect to time is

$$H(X) = -\sum_{j=1}^{t} X_{ij}/Z \; \log X_j/Z \; ,$$

the uncertainty with respect to state is

$$H(Y) = -\sum_{i=1}^{s} Y_{ij}/Z \; \log Y_i/Z \; ,$$

and the uncertainty with respect to the interaction of time and state is

$$H(XY) = -\sum_i \sum_j N_{ij}/Z \; \log N_{ij}/Z \; .$$

Predictability is defined as $P = 1 - [H(XY)/\log s - H(X)/\log s]$.

APPENDIX B

SPECIES ASSOCIATES OF N. EXILIS

TABLE XIII

SPECIES ASSOCIATES OF N. EXILIS CAPTURED DURING 1981
IN FLINT CREEK. THEY ARE CLASSIFIED AS COMMON
(C), OCCASIONAL (O), OR RARE (R).

Species	Relative Abundance	Species	Relative Abundance
Campostoma anomalum	C	Amploplites rupestris	O
Dionda nubila	C	Lepomis cyanellus	O
Nocomis asper	C	Lepomis macrochirus	C
Notropis pilsbryi	C	Lepomis megalotis	C
Notropis rubellus	C	Lepomis microlophus	R
Phoxinus erythrogaster	R	Micropterus dolomieui	C
Semotilus atromaculatus	O	Micropterus punctulatus	O
Hypentelium nigricans	O	Micropterus salmoides	O
Ictalurus natalis	O	Etheostoma blennioides	O
Fundulus catenatus	O	Etheostoma punctulatum	C
Fundulus olivaceus	C	Etheostoma spectabile	C
Gambusia affinis	C	Etheostoma zonale	O
Labidesthes sicculus	C	Percina caprodes	R
Cottus carolinae	C		

APPENDIX C

RAW DATA FOR PREDICTABILITY ESTIMATES

Climatic data from the NOAA was tabulated to aid in computations.
Monthly averages were used from 1970 to 1979 to build a matrix of the
number of times a particular state occurred during a particular month
(Tables XIV to XIX).

TABLE XIV

CLIMATIC DATA FOR LAKE CHARLES, LA.

State	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
°C												
-20 to -15												
-15 to -10												
-10 to -5												
-5 to 0												
0 to 5												
5 to 10	6	1										
10 to 15	4	8	2								4	8
15 to 20		1	8	3						1	6	2
20 to 25				7	10				3	9		
25 to 30						10	10	10	7			
30 to 35												
Prec. (mm)												
2 to 4												
4 to 8			1							1		
8 to 16				1	1					1		
16 to 32	1	1		2		1	1	1				
32 to 64	2	4	4	2	2	1	1		4	1	2	2
64 to 128	3	4	2	1	1	4	5	3	4	4	5	4
128 to 256	3	1	2	2	5	4	2	5	2	2	3	4
256 to 512	1		1	2	1		1	1		1		

TABLE XV

CLIMATIC DATA FOR SHREVEPORT, LA.

State	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
°C												
-20 to -15												
-15 to -10												
-10 to -5												
-5 to 0												
0 to 5	3	1										
5 to 10	5	4										
10 to 15	2	4	4								1	8
15 to 20		1	6	10	1						7	2
20 to 25					9	1		1	5	8	2	
25 to 30						9	10	9	5	2		
30 to 35												
Prec. (mm)												
2 to 4												
4 to 8	1									1		
8 to 16									1			
16 to 32	1	1		1		3		2	1			
32 to 64	1	3	2	3	2	1	1	3	4	1	3	2
64 to 128	3	6	5	3	3	4	4	5	1	5	4	6
128 to 256	4		3	3	5	2	5		3	3	3	2
256 to 512												

TABLE XVI

CLIMATIC DATA FOR TULSA, OK.

State	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
°C												
-20 to -15												
-15 to -10												
-10 to -5												
-5 to 0	4	2										
0 to 5	6	3										7
5 to 10		4	4								5	3
10 to 15		1	6	1						2	5	
15 to 20				9	4				1	8		
20 to 25					6	5			8			
25 to 30						5	9	10	1			
30 to 35							1					
Prec. (mm)												
2 to 4	1		1				1		1			
4 to 8	1								1			
8 to 16	1	2					2					2
16 to 32	3	3	1					1		1	3	3
32 to 64	2	1	1	3	1	1	2	3		3	1	
64 to 128	2	4	4	3	1	3	5	3	3	1	2	4
128 to 256			2	4	8	6		3	3	5	4	1
256 to 512			1						2			

TABLE XVII

CLIMATIC DATA FOR CAIRO, ILL.

State	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
°C												
-20 to -15												
-15 to -10												
-10 to -5	1											
-5 to 0	3	2										
0 to 5	6	6									1	6
5 to 10		2	6								5	4
10 to 15			4	2						3	4	
15 to 20				8	4				2	7		
20 to 25					6	4		2	7			
25 to 30						6	10	8	1			
30 to 35												
Prec. (mm)												
2 to 4												
4 to 8												
8 to 16							1		1			
16 to 32	1	1		1		1	1	1	2	1	2	1
32 to 64	2	3	1	1		2	1	1	1	4	1	
64 to 128	7	5	5	3	7	5	4	3	4	4	3	6
128 to 256		1	3	5	3	2	3	4	2	1	4	2
256 to 512		1						1				1

TABLE XVIII

CLIMATIC DATA FOR PEORIA, ILL.

State	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
°C												
-20 to -15												
-15 to -10	3											
-10 to -5	4	2										2
-5 to 0	2	7									1	6
0 to 5	1	1	7								7	2
5 to 10			3	3						2	2	
10 to 15				7	3					7		
15 to 20					6	2			8	1		
20 to 25					1	8	9	10	2			
25 to 30							1					
30 to 35												
Prec. (mm)												
2 to 4									1			
4 to 8												
8 to 16	3	1										1
16 to 32	3	3	1	2		1		3		2		
32 to 64	2	4	3		3	2	1	3	3	5	3	6
64 to 128	2	2	5	6	4	4	6	2	2	4	5	3
128 to 256			1	2	3	2	3	2	3	1		
256 to 512						1				1		

TABLE XIX

CLIMATIC DATA FOR MADISON, WI.

State	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
°C												
-20 to -15	1											
-15 to -10	5	2										
-10 to -5	3	6										1
-5 to 0	1	2	5									5
0 to 5			4	1							1	4
5 to 10			1	8							8	
10 to 15				1	7					5	1	
15 to 20					3	7			2	5		
20 to 25						2		3	8			
25 to 30						1	10	7				
30 to 35												
Prec. (mm)												
2 to 4		1							1		1	
4 to 8		1	1									1
8 to 16	4	1							1	1		1
16 to 32	2	3	1		1	1		1	2	2	2	
32 to 64	4	3	1	4	2	5	3	3	1	4	4	7
64 to 128		1	7	5	4	3	5	2	2	3	3	1
128 to 256				1	3	1	2	4	3			
256 to 512												

TABLE XX

SUMMARY DATA USED IN REPRODUCTIVE COMPARISONS

SL	ADJWT	Number of Ova	Ova/mm SL	Ova/ADJWT	Age	K ADJWT	Ova Diameter	GSI	Ovary Weight
				Cloud Creek					
58.1	3.01	40	0.688	13.29	36	1.535	3.47	308	0.9274
54.2	2.35	48	0.886	20.42	24	1.476	3.16	308	0.7256
52.3	2.34	31	0.592	13.25	24	1.636	3.24	232	0.5430
55.6	2.69	41	0.737	15.24	24	1.565	3.17	246	0.6615
47.8	2.18	31	0.648	14.22	12	1.996	1.50	37	0.0814
48.0	1.78	29	0.604	16.29	12	1.610	2.62	173	0.3080
55.3	2.97	34	0.615	11.45	24	1.756	3.48	275	0.8162
54.6	2.58	42	0.769	16.28	24	1.585	3.23	296	0.7643
47.6	1.68	23	0.483	13.69	12	1.558	2.69	129	0.2166
51.1	2.64	30	0.587	11.36	24	1.978	3.21	179	0.4716
56.2	2.91	35	0.623	12.03	24	1.639	3.52	276	0.8034
43.6	1.29	23	0.528	17.83	12	1.556	2.06	80	0.1030
50.2	2.23	32	0.637	14.35	24	1.763	3.07	232	0.5170
50.8	2.24	39	0.768	17.41	24	1.709	3.14	308	0.6900
46.8	1.88	27	0.577	14.36	24	1.834	2.46	104	0.1960
52.5	2.44	36	0.686	14.75	24	1.686	3.10	225	0.5483
				Flint Creek					
62.9	3.78	79	1.256	20.90	36	1.519	3.11	290	1.0975
55.4	2.55	45	0.812	17.65	24	1.500	2.99	224	0.5702
58.2	3.18	49	0.842	15.41	24	1.613	2.93	185	0.5897
57.4	3.20	40	0.697	12.50	24	1.692	3.14	175	0.5599
58.2	3.06	42	0.722	13.72	24	1.552	3.36	239	0.7305
52.1	2.39	34	0.652	14.22	12	1.690	2.94	202	0.4829
55.5	2.75	40	0.721	14.54	24	1.608	3.32	268	0.7386
54.8	2.57	40	0.730	15.56	24	1.562	1.72	48	0.1241

TABLE XX CONTINUED

SL	ADJWT	Number of Ova	Ova/mm SL	Ova/ADJWT	Age	K ADJWT	Ova Diameter	GSI	Ovary Weight
54.8	2.57	40	0.730	15.56	24	1.562	1.72	48	0.1241
45.6	1.31	31	0.680	23.66	12	1.382	2.16	126	0.1648
54.7	2.45	43	0.786	17.55	24	1.497	2.86	196	0.4814
47.1	1.75	28	0.594	16.00	12	1.675	1.80	52	0.0912
53.6	2.49	37	0.690	14.86	24	1.617	3.01	183	0.4550
				Green Creek					
81.2	8.31	150	1.847	18.1	46	1.552	2.70	173	1.4380
75.7	6.87	131	1.730	19.1	34	1.584	2.60	179	1.2310
71.9	5.88	137	1.905	25.3	34	1.582	2.00	102	0.6000
65.0	4.44	104	1.600	23.4	22	1.617	1.70	79	0.3500
64.3	4.10	82	1.275	20.0	22	1.542	1.90	78	0.3210
64.9	4.16	96	1.479	23.1	22	1.522	2.20	120	0.5000
61.8	4.12	71	0.997	17.2	22	1.746	1.70	61	0.2500
71.2	4.96	95	1.334	19.1	23	1.374	3.00	260	1.2910
72.0	4.54	97	1.347	21.3	23	1.216	2.80	257	1.1660
70.2	4.96	89	1.268	17.9	23	1.434	3.00	252	1.2500
65.6	3.94	95	1.450	24.1	23	1.402	2.90	309	1.2130
63.9	3.90	71	1.111	18.2	23	1.495	2.90	247	0.9620
52.7	2.04	46	0.873	22.5	12	1.394	2.70	160	0.3270
54.5	2.48	47	0.862	18.9	12	1.532	2.50	200	0.4970
55.4	2.67	53	0.957	19.9	12	1.570	2.40	143	0.3810
54.8	2.46	50	0.912	20.3	12	1.495	2.40	193	0.4740
72.6	5.02	64	0.882	12.8	25	1.312	3.10	213	1.0630
52.2	2.10	26	0.498	12.4	13	1.476	2.20	92	0.1940

VITA

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