HABITAT SELECTION AND ITS RELATION TO REPRODUCTIVE DEVELOPMENT
OF
THE ROUGH SKINNED NEWT, *Taricha granulosa* (Skilton)
ON
SOUTHERN VANCOUVER ISLAND

by

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ABSTRACT

The rough-skinned newt was studied from 1970 to 1973 at a permanent pond near Victoria, British Columbia, to determine its reproductive development, especially during the nonbreeding season, in relation to habitat selection differences observed between males and females. Newts were sampled on land by hand and trapping, in the lake during SCUBA dives and by attraction to a nightlight. Animals were toe-clipped for easy recognition on recapture. The data indicated that normally adult males are permanently aquatic, while adult females are terrestrial during the nonbreeding season, from September to March, and that individuals could breed in successive years. In 1972, a year of low rainfall, some males overwintered on land while some females remained in the lake. Analyses of morphologic secondary sex character and gonad histology suggested that males overwintering in the lake and females overwintering on land could fully mature reproductively the following breeding season. Males overwintering on land and females overwintering in the lake could not. It is speculated that climatic factors partly account for these observations.

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INTRODUCTION

Reproductive success in animal populations is often related to environmental conditions prevailing during the nonbreeding season (Brenner, 1969; Shoop, 1967; Tchou and Wang, 1963). Recently, an increasing number of studies on amphibians (Gray, 1971; Hurlbert, 1969; Cooper, 1956; Hendrickson, 1954; Neill, 1948; Hamilton, 1948) has shifted an earlier emphasis on delineating reproductive strategies to investigating the relation between nonbreeding activity patterns and the reproductive cycle. A major aim of the present work is to relate habitat selection during the nonbreeding season with reproductive development in the rough-skinned newt, *Taricha granulosa* (Caudata:Salamandridae) on Southern Vancouver Island.

Pimentel (1960) in Oregon and Efford and Mathias (1969) on the British Columbia mainland have shown similar postbreeding habits for both male and female adults of *T. granulosa*. Both sexes of *T. rivularis* and *T. torosa* also migrate overland from aquatic breeding sites (Stebbins, 1951; Chandler, 1918; Ritter, 1897) and spend the nonbreeding season in wood piles, rotten logs, and subterranean locations. The following breeding season, adults return to water. Preliminary observations on South Vancouver Island adjacent to the British Columbia mainland suggest that *T. granulosa* shows sexually dimorphic behaviour with males remaining aquatic and females overwintering on land. This behaviour is documented in the present study and its effects on sexual maturation are investigated.

In addition to a general description of the life history of *T. granulosa* on Southern Vancouver Island this report focuses on several specific reproductive questions:

1. Do individuals breed in successive years? In California and Oregon, populations of both *T. torosa* and *T. granulosa* breed annually but individuals apparently breed every second year (Pimentel, 1960; Miller and Robbins, 1954). By contrast, some individuals of *T. rivularis* breed in consecutive years, as do individuals of *T. granulosa* on the British Columbia mainland (Efford and Mathias, 1969).
2. What is the seasonal timing of various reproductive activities, including migration, breeding, ovulation, egg deposition and egg development? *T. torosa* and *T. rivularis* lay their eggs in clusters (Stebbins, 1954a; McCurdy, 1931). *T. granulosa* deposits eggs singly over an extended period of time (Chandler, 1918).
3. What is the histologic picture of gonad development on a seasonal basis and how is it correlated with changes in externally visible sexual characteristics?

MATERIALS AND METHODS

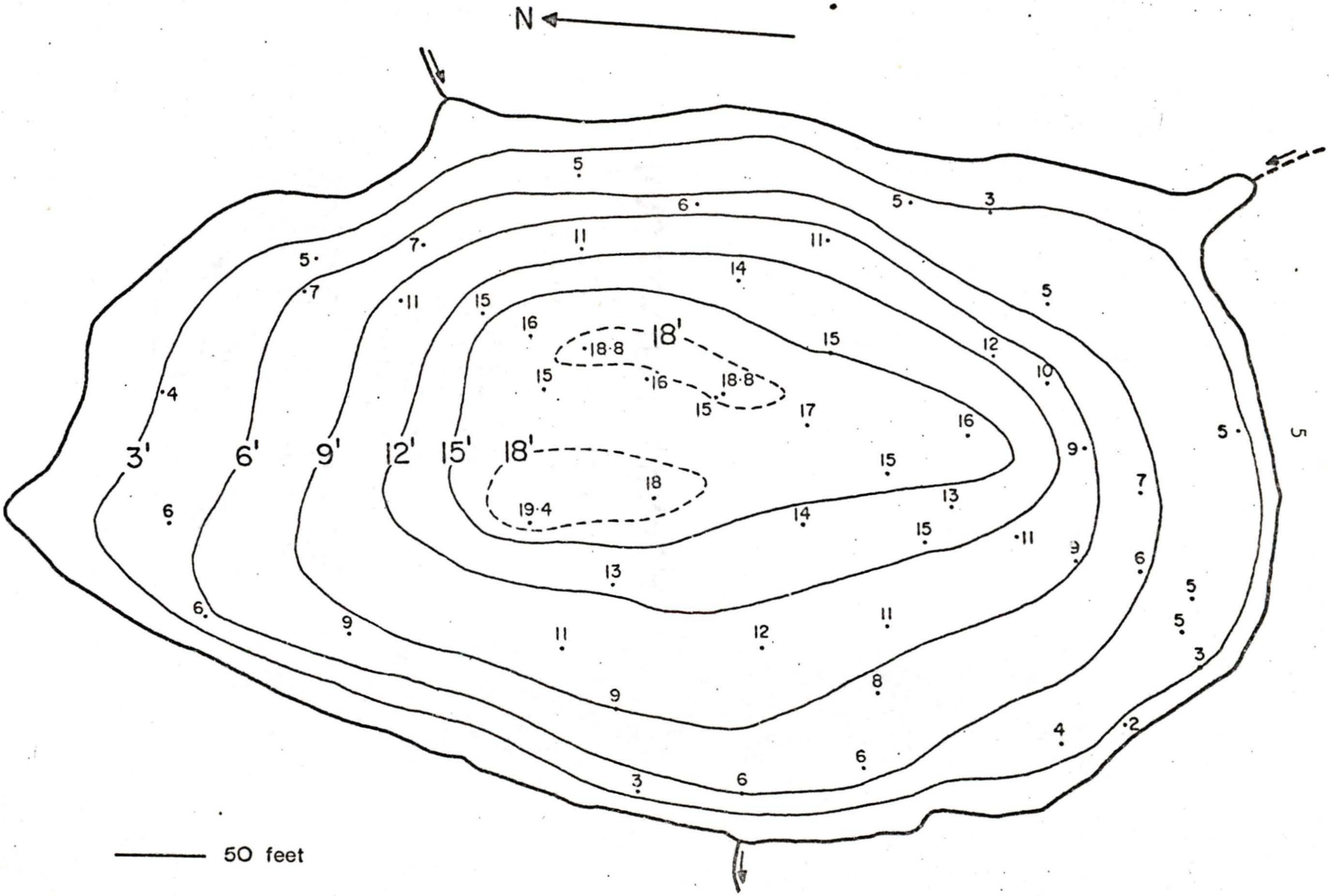
Study Area

All data were collected from a 743 acre study area at Blinkhorn Lake, a permanent, moderately eutrophic freshwater pond in the Metchosin District of British Columbia. The lake (Fig. 1) is located about fifteen miles southwest of Victoria on the southern tip of Vancouver Island. Watershed and morphometric characteristics are summarized in Appendix 1 and Figure 2. Area and volume characteristics are given in Appendix 2. Blinkhorn Lake is part of the Insular Lowland Limnological Region (Northcote and Larkin, 1963) located in the Pacific Coast Mesothermal Forest Region (Krajina, 1965). Aquatic vegetation is given in Appendix 3 and the dominant terrestrial vegetation in Appendix 4.

Climatically the region is classed as Cool Summer Mediterranean (Chapman, 1952). Annual precipitation is about 40 inches (Roemer, 1972). Most of this falls from mid-September through April. However, record dry weather was recorded in 1972 and 1973 (Environment Canada, 1974). The short summer, from June through mid-September, is generally dry. The mean annual temperature is 50°F. The moderating effect of the nearby ocean normally keeps summer temperatures below 80°F and winter temperatures above freezing. The number of frost-free days in the area is about 330. Snow falls infrequently during late December, January, and February, normally remaining on the ground for periods of less than two weeks. Occasionally an ice cover up to two inches thick forms on the lake.

FIGURE 1. Blinkhorn Lake.

FIGURE 2. Blinkhorn Lake morphometry (Hagmeier, E.M. and Limnology 426 class, 1972).


N
3'
6'
9'
12'
15'
18'
18'
18·8
18·8
19·4
50 feet

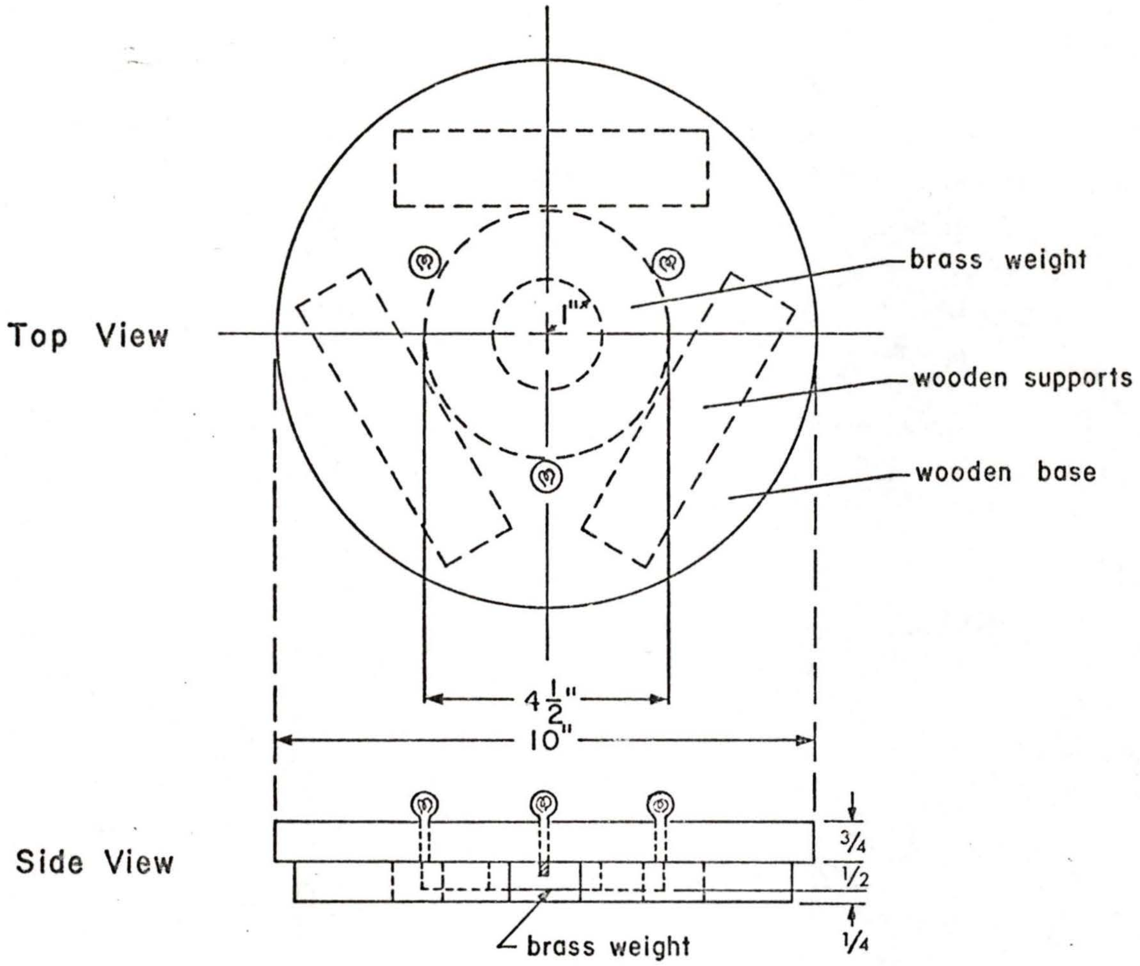
Sampling Methods

A nightlight was used to attract newts in the lake from November, 1970 through April, 1972, in 56 of 72 weeks. Captured animals were checked for sex and secondary sex character development. The apparatus consisted of a triangular array of three lights (Fig. 3) powered by a 12-volt automobile battery left on shore. The base was painted green, the colour found to blend best with the newts' environment, since animals avoided black or white bases. At sunset the array was placed on the lake bottom into approximately 70 cm of water 3 m from the lake shore. A long-handled dip-net was used to capture newts attracted to the lights.

SCUBA diving was employed to collect information on newt density, distribution, habitat utilization, secondary sex character development, and sex ratios within the lake. *T. granulosa* was observed and photographed in its natural underwater habitat during daylight on six occasions from November 19, 1972, to June 4, 1973. Nearly the entire lake bottom was examined on each occasion.

To sample migrating newts for sex and state of reproductive development on land, a drift fence (Storm and Pimentel, 1954) extended for 400 meters along an abandoned logging road on the east side of Blinkhorn Lake (Figs. 4 and 5). This funneled a portion of the newt population into traps from March, 1972 to May, 1972 and September, 1972 to September, 1973. Traps were removed from May to September, 1972 to deter vandalism. In the fall of 1972 a second 25 meter fence was established bisecting a two acre meadow fronting on the south lake shore. It was abandoned in 1973 due to low trapping success. The fencing,

FIGURE 3. The nightlight apparatus used to attract newts.


Top View
1"
brass weight
wooden supports
wooden base
4 1/2"
10"
Side View
3/4
1/2
1/4
brass weight

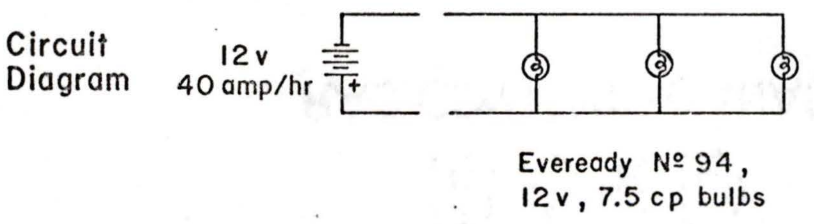

Circuit Diagram
12 v
40 amp/hr
+
Eveready № 94,
12 v, 7.5 cp bulbs

FIGURE 4. Drift fence location (white dots) at Blinkhorn Lake.

FIGURE 5. A portion of the drift fence and traps.

④

⑤

23 cm high with 3 cm buried underground, was constructed of PVC window screening. The screening was stapled at 1.2 m intervals to 60 cm high stakes.

Ten traps used in a pilot study in the spring of 1972 were augmented in the fall by an additional 30 inserted in prepared openings at intervals 6 to 12 m along the fence. Trap frames were made of 3 mm copper-coated welding rod. A center partition and the outside of each trap were covered with PVC screening and secured around the frame with sailmaker's nylon thread. Molded, trapezoid-shaped funnels of fiberglassed roving were sewn into both ends of each trap as entrances. The finished trap, 61 cm long, 30.5 cm wide, and 15 cm high, was placed in a fence opening with one funnel facing away from the lake and the other toward it. Animals taken from the lake side of the traps were assumed to be travelling from water to land, and those from the land side, from land to water. It was assumed that trapping effieiency was the same for all traps. The number of animals trapped was presumed indicative of the relative numbers of migrating animals.

Juveniles, newly metamorphosed newts that spend three to four years on land before becoming sexually mature (Stebbins, 1954a), were only censused.

For easy recognition on recapture, captured newts were toe-clipped at the base of digits with a pair of manicure scissors. Marking took place from March, 1972 to the end of the study. Animals captured and released in the lake had all toes on the left front foot removed. Animals captured in traps and released in the direction of travel had all toes on the right front foot removed. Fifteen males and three females caught in traps in fall, 1972 moving away from the lake also had all toes on the left hind foot removed, and were returned to the lake to determine what proportions would remigrate or remain in the lake. The orignal capture place of any recaptured animals was thus easily determined. Unmarked animals presumably had not been previously encountered. Trapped animals received in addition, toe clips for individual recognition. About half the animals were treated by immersing severed digits in a .1 N solution of the regeneration inhibitor, beryllium nitrate ($BeNO_3 \cdot 3 H_2O$) (Heatwole, 1961) for thirty seconds. A year later, even untreated recaptures could be easily identified. Less than half of each of the severed toes and some cartilage was regenerated.

Weather recording

A Kahlsico hygrothermograph located near the southwest corner of Blinkhorn Lake under an abandoned log cabin recorded temperature and relative humidity continuously from September, 1972 to September, 1973. Land and water temperatures for this period are given in Appendix 5. Precipitation was measured using a standard rain gauge (Appendix 6).

External Morphology and Histology

Smith (1927) briefly described the gross anatomy of the urogenital system in *T. granulosa*. McCurdy (1931) presented the anatomy and histology of the *T. torosa* urogenital system. Their findings are treated as reference points in comparison with new findings on the reproductive development of *T. granulosa*.

Adult male and female animals were classified reproductively according to their external morphology and time of capture. Females always possess granulose or papillated, terrestrial integument. They were designated either gravid, nongravid, or, in a few cases, semigravid. Nongravid females had no lateral swelling of the posterior body. Oocytes for such females as were examined were small, requiring at least four months to become fully mature. Gravid and semigravid females, or those whose eggs would probably mature in less than four months had a noticeable lateral body swelling anterior to the cloaca due to the presence of enlarging ova. Field animals were compared to dissected females for accuracy.

Adult males were designated as either nonbreeding, semibreeding, or breeding animals. Nonbreeding males exhibited the nonbreeding female morphology, with papillated skin, a flat or nearly flat vent as seen in profile, and little or no tail crest. Such animals captured in summer were termed postbreeding males. Semibreeding and breeding males possessed a variable combination of four secondary sexual characteristics: swollen vent, high tail crest, smooth aquatic skin, and cornified, melanized nuptial pads. These characteristics appear in the order given and disappear in reverse order. Semibreeding males lacked one, two, or three of these characteristics. Semibreeding males were classified as prebreeding when they showed one or more of these characteristics in late winter to early spring, or postbreeding if captured in late spring.

The accuracy of the reproductive classification based on external features of field animals was checked by histologic analyses of selected newts. One or two animals were used to represent the majority of those captured. Any externally deviant individuals were also sectioned and included.

Kidneys, rete apparatus, gonads, and fat bodies of 44 adult males and 32 adult females were excised within 24 hours of capture from February through November, 1973. Tissues were kept pliable even after several months in the fixative by adding three or four drops of glycerin to each four dram vial containing 10% formalin. Location and date of capture, direction of travel if applicable, and external morphology were recorded for each animal. Body weight of towel-dried animals with the bladder contents expelled, snout-vent length from tip of nose to anterior vent opening and total length were recorded for most animals.

Serial sections of gonads and ducts were prepared from paraffin-embedded tissue using a modified technique of Galigher and Kozloff (1964, Appendix 7). Penetration appeared uniform for all blocks of tissue up to 10 mm^3. For each female, a 5 - 10 mm section of ovary and a similar length of midoviduct were prepared. For each male from one to three testis lobes with strands on one side and a 5 - 10 mm section of mid sperm duct were prepared. Most males had a multiple testis, of more than two lobes. All tissues were sectioned at 8 microns, stained with Harris' hematoxylin, counterstained with eosin, and serially mounted on slides. Cross sections of all ovaries and sagittal sections of all lobes were prepared. Meyer's albumin was used as an adhesive, and Histoclad as a mounting medium. A black background for spreading permitted all sections to be seen easily. A lower spreading temperature of 34 - 36°C as compared to the normal 37°C allowed nearly all sections to spread evenly and become nearly wrinkle-free.

RESULTS

Some Life History Aspects

Oliver and McCurdy (in press) outlined the normal annual life cycle of *Taricha granulosa* at Blinkhorn Lake on southern Vancouver Island. Adult males usually remained aquatic throughout the year and semiactive even in winter while females spent the nonbreeding season overwintering on land.

Males began to mature sexually in autumn, as shown in Table 1. Spermatophores (Davis and Twitty, 1964) were produced from mid-March to late April. On May 3, 1973, fifty of 81 males collected from the lake were still in breeding condition. Only four males had a flaccid vent, which according to Riemer (1958) suggests that they were still engaged in courtship activity. Twenty-seven were in postbreeding condition, with no nuptial pads, vent and tail crest reduced in size, and only turgid skin apparent.

Male breeding activity ceased entirely by mid-May: animals taken from the water after this time have lost most of their secondary sexual characteristics. Thus of 67 males taken on June 4, 1973, eight already had granulose skin and none remained in breeding condition. Despite attaining the postbreeding external morphology typical of terrestrial females, most males in Blinkhorn Lake remained aquatic indefinitely.

Females migrated from terrestrial overwintering locations to the breeding site. A few arrived at the breeding pond in late January or February, 1973, when the winter was mild and very rainy. However, most females migrated to the water during the usually wet and mild period

TABLE 1. *Taricha granulosa* MALE SECONDARY SEX CHARACTER DEVELOPMENT.

NB = Nonbreeding, SB = Semibreeding, B = Breeding

Date	Character	Assigned Reproductive State
July-Sept.	Terrestrial granulose skin becoming aquatic and turgid, flat nonbreeding vent swelling	NB to SB
Oct.-Dec.	Turgid aquatic skin and bulbous vent of breeding males present tail crest enlarging	SB
Dec.-mid-Jan.	Turgid aquatic skin, bulbous vent, and high tail crest of breeding males present, nuptial pads developing	SB
mid-Jan.-April	Turgid aquatic skin, bulbous vent, high tail crest, and nuptial pads present	B
May	Nuptial pads disappear, tail crest and vent reduced in size, aquatic skin still evident	B to SB
June	Nuptial pads, tail crest not present vent flattened in profile, terrestrial papillated skin develops	SB to NB

from mid-March to mid-April. For example, in the 1972 breeding migration, 231 of 266 females were trapped between March 10 and April 1 (Table 2).

Females usually remained in the breeding pond during the dry summer months until the first rainfall, normally in mid-September. However, on August 17 and 18, 1973, thirty-one females were captured at the drift fence migrating away from the lake after one-third inch of rain had fallen, the first in forty days. Dissection revealed that no oviducal eggs remained, with five to ten ovarian eggs per side almost fully degenerated. Eggs remaining in the ovary were small, of varying sizes, and only lightly pigmented, indicating that yolk deposition was just beginning.

Most females and newly metamorphosed juveniles left the lake during the wet fall months of September and October, as shown for 1971 in Table 2. The last few animals in 1973 left the breeding pond in mid-November before the advent of freezing weather (Table 2).

Migration

No postbreeding males were seen or captured migrating away from the lake in the autumn of 1971. About nine hundred juveniles and three hundred adult females were observed migrating away from the lake during or after heavy, sustained rainfalls in early autumn of 1971 (Table 2). Adult ovaries each contained five to ten degenerating eggs and numerous small, largely unpigmented eggs, indicating that the females were post-reproductive. The following spring (1972) ten traps at the drift fence yielded over two hundred females, but only one male migrating back to the lake. The females were all gravid. The male was in semibreeding

TABLE 2. *Taricha granulosa* CAPTURED WHILE MIGRATING ON LAND IN THE BLINKHORN LAKE AREA, 1971 - 1973.

Animals taken from mid-November through July were moving from terrestrial overwintering sites to the lake. Animals taken from August through early November were moving away from the lake to overwinter on land. (- means no collections made)

	nonbreeding						semibreeding						breeding								
	males			females			males			females			males			females			juveniles		
	71	72	73	71	72	73	71	72	73	71	72	73	71	72	73	71	72	73	71	72	73
Nov. 16-30	0	27	-	0	-	-	0	0	-	0	1	-	0	0	-	0	0	-	0	0	-
Dec.	0	10	-	0	0	-	0	0	-	0	1	-	0	0	-	0	0	-	0	0	-
Jan.	-	-	12	-	-	0	-	-	0	-	-	1	-	-	0	-	-	0	-	-	0
Feb.	-	-	114	-	0	0	-	0	0	-	0	6	-	-	0	0	4	0	-	-	0
Mar.	-	0	86	-	0	0	-	0	6	-	0	0	-	0	1	-	231	424	-	0	0
Apr.	-	0	12	-	0	0	-	1	10	-	0	0	-	0	0	-	35	360	-	0	0
May	-	0	7	-	0	0	-	0	1	-	0	0	-	0	9	-	9	10	-	0	0
June	-	-	4	-	-	0	-	-	0	-	-	0	-	-	0	-	-	3	-	-	0
July	-	-	4	-	-	0	-	-	0	-	-	0	-	-	0	-	-	0	-	-	0
Subtotal	0	37	239x	0	0	0	0	1	17	0	2	7	0	0	1	0	266	807	0	0	0
Aug.	-	-	0	-	-	92	-	-	0	-	-	0	-	-	0	-	-	0	-	-	2
Sept.	0	36	-	30	21	-	0	3	-	0	0	-	0	0	-	0	0	-	7	250	-
Oct.	0	33	-	69	15	-	0	7	-	0	0	-	0	0	-	0	0	-	49	25	-
Nov. 1-15	0	28	-	1	2	-	0	2	-	0	0	-	0	0	-	0	0	-	0	7	-
Subtotal	0	97	0	100+	38	92	0	11	0	0	0	0	0	0	0	0	0	0	56*	282	2

x = approximately one-third were first year adult males
+ = approximately three hundred females also observed
* = approximately nine hundred juveniles also observed

condition with smooth skin and a slightly enlarged vent.

The migration data indicated that in certain years only metamorphosed juveniles and postreproductive females overwintered on land.

A departure from this apparently normal migratory pattern occurred in 1972 and 1973. Some males migrated away from the lake and apparently overwintered on land, while some females remained throughout the winter months in Blinkhorn Lake (Tables 2 and 4) when rainfall was sporadic (see Appendix 6). Over half the adults who reached the fence during periods of scant or no rainfall were found dessicated the day following their initial movement. Some died even before entering the traps.

From mid-September to early November, 1972, adult male migrants outnumbered female migrants by nearly 4:1 (see Table 2). All females were in postbreeding condition. Eleven males in semibreeding condition had a smooth aquatic skin and slightly enlarged vent. Ninety-six males were in the terrestrial, nonbreeding state. The last fall migrant in nonbreeding condition, left the lake on November 12, 1972. Males remaining in the lake possessed all breeding characteristics except nuptial pads on November 19, 1972. Probably many migrants escaped during intense migration from September 14 to 22, 1972 when eighteen of forty traps were vandalised. Newts also escaped capture during March 22 - 28, 1973, when ten traps were destroyed.

Sub-freezing temperatures in December and January did not deter newt migration. Animals moved even when patchy snow covered the ground. Periods of heavy rainfall alternated with dry periods in December, 1972 and January, 1973 (Appendix 6). Humidity remained above 50% from September 1 to December 1, 1972, and apparently did not influence newt migration.

About 10% of the animals marked in the 1972 fall migration moving away from the lake were recaptured in spring, 1973 returning to the breeding pond. Granulose males began returning to the lake November 23, 1972. Some nonbreeding males were captured in December and January (Table 2). Males in large numbers and still in nonbreeding condition returned to the lake in February, 1973. Approximately one-third of these males were newly adult, of small size and granulose integument (Table 2). On March 7, 1973 the first three males with smooth skin, swollen vents, and enlarging tail crests of prebreeding males were taken. Before this date all males taken on land were in nonbreeding condition externally. In April, 1973 fewer granulose males and increased numbers of smaller semibreeding males were captured. The former probably were mature males that had bred in 1972, and spent the following winter on land. The latter were perhaps newly matured males returning to water for the first time after spending three or more years on land as juveniles. The last three such males were captured moving overland toward the breeding pond July 10, 1973. No animals were captured moving toward the lake after this date.

As in the 1971 and 1972 breeding migrations, all migrating females appeared gravid or nearly so, arriving in large numbers starting the second week in March, 1973 (Table 2). These females were captured moving overland toward the breeding pond. It is assumed that they overwintered on land.

Table 3 correlates newt movement with rainfall. It shows that most adults and juveniles migrated during rainy periods.

TABLE 3. PRECIPITATION AND *Taricha granulosa* TRAPPED ON LAND. TOTAL NUMBER OF THREE CONSECUTIVE DAY PRECIPITATION GIVEN IN PARENTHESES.

Precip., in.	0 - .1			.1 - .4			.4 - 1.0			1.0 - 1.4			1.4 plus		
Dates	no. adults	no. juv	no. 3-day periods	adults	no. juv	no. 3-day periods	adults	no. juv	no. 3-day periods	adults	no. juv	no. 3-day periods	adults	no. juv	no. 3-day periods
Mar 1-May 1, 1972[1]	32	0	(5)	146	0	(2)	36	0	(2)	0	0	(0)	0	0	(0)
Sep 1-Nov 15, 1972[2]	12	16	(16)	51	53	(5)	16	38	(2)	23	7	(1)	35	168	(1)
Nov 16, 1972-Aug 1, 1973[1]	413	0	(63)	420	0	(28)	169	0	(13)	14	0	(1)	15	0	(2)
	457	16	(84)	617	53	(35)	221	38	(17)	37	7	(2)	50	168	(3)
$\bar{X}$ no. newts/ 3-day interval	5.44	.19		17.62	1.51		13.00	2.23		18.50	3.50		16.67	56.00	

[1] migration toward Blinkhorn Lake

[2] migration away from Blinkhorn Lake

TABLE 4. *Taricha granulosa* CAPTURED IN BLINKHORN LAKE, 1970 - 1972.

(- means no collections made)

	nonbreeding								semibreeding								breeding							
	males				females				males				females				males				females			
	70	71	72	73	70	71	72	73	70	71	72	73	70	71	72	73	70	71	72	73	70	71	72	73
Nov.	5	0	3	-	0	4	7	-	101	11	26	-	0	0	5	-	0	0	25	-	0	0	0	-
Dec.	0	0	-	-	1	0	-	-	10a	10	-	-	0	0	-	-	0	0	-	-	0	0	-	-
Jan.	-	0	0	0	-	0	1	4	-	39	2	3	-	0	2	0	-	4	7	17	-	0	0	0
Feb.	-	0	0	-	-	0	0	-	-	15a	1	-	-	3	0	-	-	31a	34	-	-	2	4	-
Mar.	-	1	1	5	-	1	1	5	-	1	3	18	-	0	0	12	-	18	149	179	-	2	5	9
Apr.	-	0	5	-	-	0	2	-	-	0	0	-	-	0	0	-	-	22	240	-	-	4	53	-
May	-	-	-	0	-	-	-	0	-	-	-	27	-	-	-	3	-	-	-	54	-	-	-	40
June	-	4a	-	9	-	0	-	0	-	4a	-	58	-	0	-	3	-	0	-	0	-	1	-	44
July	-	2a	-	-	-	5a	-	-	-	13a	-	-	-	12a	-	-	-	0	-	-	-	0	-	-
Subtotal	5	26	9	14	1	10	10	9	111	93	32	106	0	69	7	18	0	75	455	250	0	9	61	93
Aug.	-	2	5	-	-	4	2	-	-	4	2	-	-	0	0	-	-	-	0	-	-	0	0	-
Sept.	-	0	-	-	-	5	-	-	-	5	-	-	-	0	-	-	-	0	-	-	-	0	-	-
Oct.	-	0	-	-	-	4a	-	-	-	14a	-	-	-	0	-	-	-	0	-	-	-	0	-	-
Subtotal	-	2	5	-	-	13	2	-	-	23	2	-	-	0	0	-	-	0	0	-	-	0	0	-

a = Estimated

Blinkhorn Lake newts apparently followed no definite migration routes (Table 5). They radiated outward from the lake in fall and apparently reversed direction in spring. A few hundred animals observed moving away from the lake in September and October, 1971 and toward the lake in March, 1972 travelled singly or in widely spaced groups of less than ten animals along a one mile arc extending around three quarters of the lake shore. The last largely inaccessible quarter was not examined. Migrating newts followed no definite pathways or directional orientation.

Aquatic Habitat

Newts captured in the lake (Table 4) from November to March, 1970 - 71 and 1971 - 72 included 29 females, 326 males, and no juveniles. Eleven females captured in January and February 1971 and 1972 apparently overwintered on land, arrived at the breeding pond early, and were nearly gravid or gravid. Thirteen were nonbreeding females overwintering in the lake, while five were semibreeding. In November, 1970, 106 males and in January, 1971, 43 males but no females were captured. All but five males were semibreeding or breeding animals. The data indicated that males remained in Blinkhorn Lake and matured sexually the following breeding season, while females did not.

Table 6 shows the density and distribution of the lake animals. Most males overwintered in Blinkhorn Lake apparently by burying themselves in the flocculent mud of the bottom. Some rested their entire bodies on the bottom surface, while others were buried with their heads protruding from the mud. Many were apparently entirely buried under the

TABLE 5. ANIMALS TRAPPED ON LAND DURING THE FALL AND SPRING MIGRATION, 1972 AND 1973.

FIGURE 5 (PAGE 8) ILLUSTRATES THE DRIFT FENCE WHERE TRAPS WERE LOCATED.

Trapped newts moving from lake to land September 18 - November 21		Trapped newts moving from land to lake November 23 - June 13	
Trap	No. newts	Trap	No. newts
1-4	2	1-4	5
5	1	5	56
6	0	6	16
7	1	7	27
8	5	8	9
9	4	9	43
10	7	10	18
11	14	11	10
12	6	12	21
13	6	13	17
14	4	14	32
15	1	15	41
16	2	16	71
17	2	17	36
18	0	18	52
19	2	19	10
20	2	20	25
21	8	21	35
22	7	22	20
23	5	23	52
24	4	24	8
25	12	25	97
26	13	26	27
27	9	27	36
28	3	28	34
29	7	29	4
30	2	30	46
31	7	31	58
32	4	32	33
33	6	33	27
34	2	34	16
35	11	35	20
36	7	36	34
37	11	37	16
38	7	38	14
39	5	39	23
40	7	40	15

TABLE 6. *Taricha granulosa* OBSERVED IN BLINKHORN LAKE.

+ OCCASIONALLY A GROUP OF 4-5 NEWTS/METER^2 WAS OBSERVED.

Date	Newt density	Distribution
Nov 19/72	1/m^2	uniform, 6-16 foot depth
Jan 21/73	2-3/½m^2	clumps in mud every 3-5 m., 12-16 ft. depth
Mar 4/73	6-8/m^2	clumps in mud 12-16 ft. depth and
	3-4/m^2	8-12 ft. depth every 5 m.
Mar 18/73	4-10/m^2	clumped every 3-4 m., 8-16 ft. depth
May 3/73	6/m^2	uniform, mud-plant border, 8-16 ft. depth
	1/m^2	2-8 ft. depth, plants
	3-4/m^2	2-3 ft. depth
June 4/73	1-2/m^2	uniform, 3-16 ft. except at mud-plant border from
	2-3/m^2	8-12 ft. depth, uniform

mud leaving numerous pockmarks etched on the bottom (Figs. 6 and 7).

On January 21, 1973, few newts were visible in the lake but on March 4, 1973, they were very numerous as the breeding season was beginning. Most of the newts were lake-overwintered males in breeding condition and the remainder were over half the land-overwintered males that had passed through the drift fence. Only twelve land-overwintered females, all gravid, reached the drift fence before March 4. Six of these were sacrificed. The remaining six were allowed to resume their pondward migration. Thus very few, if any, land-overwintered females were in the lake on March 4. Of fourteen females captured in the lake, all but one probably overwintered there. Their skin was still papillated, but much less than terrestrial females' skin. It resembled the smoother, turgid skin of aquatic males. Eight of thirteen bulged slightly, as if their eggs were still developing. The remainder were nongravid. Probably none of these females would fully mature sexually during 1973.

Male-male pairings were common in the winters of 1970 - 1971 and 1971 - 1972, when about 10% of the lake animals captured in January and February were in homosexual pairs. One such pair was observed on March 4, 1973, when three male-female pairs were also spotted. Aggressive males on top were all large and in breeding condition, submissive males on bottom smaller and in semibreeding or breeding condition. Three males had flaccid vents indicating intense courtship activity (Riemer, 1958), and perhaps had recently deposited spermatophores. The largest female had a white spermatophore plug in her vent. Animals other than paired newts were not in contact with each other. Newts in the vegetation were sluggish, while those on the open mud were quite active,

FIGURE 6. Newt burrowing into mud at the bottom of Blinkhorn Lake.

FIGURE 7. Mud depression (arrow) covering a newt on the bottom of Blinkhorn Lake.

FIGURE 8. *Taricha granulosa* underwater, a homosexual male pair.

6

7

8

squirming into the mud as the diver approached.

While about 15% of the newts were in the vegetation on March 18, 1973 very few animals were observed among plants two weeks earlier. *Ceratophyllum demersum* was preferred as plant habitat (Fig. 9). Newts were rarely found among other aquatic plant species (Appendix 3). Some gravid land-overwintered females apparently entered the lake by March 18, 1973, when some homosexual male pairs were still observed (Fig. 8). Pairs of males were often seen fighting on our just above the lake bottom. Eighteen heterosexual pairs were sighted, all but one on the open mud. All newts, including pairs, rested on top of the mud or on plants until disturbed by the divers. They then dove straight into the mud, just under its surface.

Pairing and courtship apparently occur in deeper water away from shore. Males with flaccid vents indicating intense courtship activity and females with spermatophores were only observed on the open mud (Table 7) in deeper parts of the lake.

Most courtship activity had ceased by May, 1973. Only two male-female pairs among approximately 400 newt sightings were observed. Male transformation from a breeding to a semibreeding condition occurred rapidly. Of 54 breeding males taken into the laboratory on May 3, 1973 all lost the nuptial pads, half lost the tail crest, and seventeen attained the terrestrial morphology within ten days. Similarly, no males in the lake one month later were in breeding condition. On this date no pairs were sighted, as mating activity had ceased.

TABLE 7. NEWTS TAKEN FROM BLINKHORN LAKE MAY 3, 1973

PAIRING AND COURTSHIP OCCURRED ON THE OPEN MUD.

B = BREEDING SB = SEMIBREEDING

Location	No. Males	External Reproductive Condition	No. Females	External Reproductive Condition
Vegetation	19	12B 7SB	9	9B
Mud	28	25B* 3SB+	27	27B#
Mud-Vegetation	34	17B 17SB	17	14B 3SB

* - 2 males with flaccid vents, seventeen in heterosexual pairs

\+ - nuptial pads lost

\# - one female with spermatophore plug in her vent

FIGURE 9. Newt hiding among *Ceratophyllum demersum* at a ten-foot depth. Newts preferred this plant species for shelter, especially at the mud - vegetation border.

Egg Development and Deposition

Eggs began enlarging in September, but did not all develop at the same rate. A few large eggs were found in ovaries in January, but these did not become fully mature until April.

T. granulosa exhibited an extended breeding season. Eggs were apparently deposited discontinuously over a period of several weeks. Individual females apparently deposited only a few eggs per day for a few consecutive days, and then deposited no more eggs for several days. The entire population apparently deposited eggs on certain days but not on others. Eggs are deposited in this start-and-stop manner from mid-April to early July. Thus embryos and larvae late in the breeding season were found in discontinuous stages of development, each stage separated in time from the succeeding one by a period of several days. On May 3, 1973, all eggs collected from Blinkhorn Lake were in the early neural plate stage as seen through the transparent jelly coats. Eggs were laid individually. Each egg is placed in the crotch of a leaf node (Fig. 10). Most (90%) eggs were deposited on *Ceratophyllum demersum*, with leaves of this plant often incorporated into the jelly capsule.

One month later, 40 of 47 females collected in the field and examined on the same day still contained a large complement of mature eggs in both ovaries, a maximum of three eggs in each oviduct, and no eggs in peritoneal cavity. This indicated that these oviducal eggs were about to be deposited when the females were captured. Only freshly deposited eggs were seen that day, while two larvae, presumably in the neural plate stage in May, were observed among *Ceratophyllum demersum* on the lake bottom on June 4, 1973.

FIGURE 10. Embryo in the early neural plate stage (arrow) taken from Blinkhorn Lake May 3, 1973. Water temperature 17°C. Neural plate (arrow), jelly capsule (J), and node of *Ceratophyllum demersum* (C) are indicated.


3
C
J

Females deposited eggs in the absence of breeding males. Females store sperm in cloacal spermathecae. Sperm from spermatophores deposited by breeding males was not obtained after May. Eggs are fertilized within the female as they travel through the oviduct past the spermathecae.

Recapture Data

Ninety-four marked newts were recaptured during the study. These animals revealed patterns of movement and reproductive development within the population (Tables 8 - 11). Males taken in the lake in fall were in semibreeding condition and attained the breeding condition by early February. Three males (A, B) in semibreeding condition in October and November had not developed the tail crests of breeding males when recaptured in November and January. Three males in semibreeding condition marked at the same time as the other three had transformed to breeding animals when recaptured in February and March (C - E, Table 8). Thus the nuptial pads of breeding males develop in the period from late January to early February.

Five males captured in the lake in 1972 and recaptured in 1973 were in breeding condition both years (G, J, M, Table 8), thus indicating breeding occurs in consecutive years. Two semibreeding males marked November 21, 1972 were also in breeding condition on May 3, 1973 (F, Table 8). Of ten mature males taken from the lake and kept in the laboratory from April 2 to October 2, 1972 before being released again, eight matured sexually the following spring despite their captivity (G, I - K, Table 7). Other males kept in the laboratory did not mature reproductively. This indicated sexual development was retarded during the six month laboratory confinement. Two of the ten (H, L, Table 8)

TABLE 8. *Taricha granulosa* CAPTURED AND RECAPTURED IN BLINKHORN LAKE. ** = ANIMALS TAKEN FROM LAKE AND KEPT IN LAB UNTIL OCTOBER 2, 1972, WHEN THEY WERE RETURNED TO THE LAKE.

+ = POSTBREEDING MALE

Code	No.	Sex	Date of Original Capture	Original Reproductive Condition	Date Recaptured	Recapture Reproductive Condition
A	1	Male	Oct/71	SB?	19 Nov/72	SB
B	2	"	19 Nov/70	SB	12 Jan/71	SB
C	1	"	25 Nov/70	SB?	2 Feb/71	B
D	1	"	Oct/71	SB	24 Feb/72	B
E	1	"	21 Nov/72	SB	18 Mar/73	B
F	2	"	21 Nov/72	SB	3 May/73	B
G	1	"	2 Apr/72	B	4 Mar/73	B**
H	1	"	2 Apr/72	B	4 Mar/73	SB**
I	1	"	2 Apr/72	B	18 Mar/73	B**
J	2	"	2 Apr/72	B	3 May/73	B**
K	4	"	2 Apr/72	B	4 Jun/73	SB+
L	1	"	2 Apr/72	B?	4 Jun/73	NB**
M	1	"	12 Mar/72	B	3 May/73	B
M	1	"	12 Mar/72	B	3 May/73	SB+
N	1	"	18 Mar/73	B	4 Jun/73	SB+
O	1	Female	Mar/71	B	1 Mar/72	B
P	1	"	2 Apr/72	B	4 Mar/73	B**
Q	1	"	12 Mar/72	B	4 Jun/73	B
R	1	"	3 May/73	B	4 Jun/73	B

TABLE 9. *Taricha granulosa* CAPTURED ON LAND AND RECAPTURED IN BLINKHORN LAKE. ++ = ANIMAL WAS RETURNED TO LAKE TO OVERWINTER.

Code	No.	Sex	Date of Original Capture	Original Reproductive Condition	Date Recaptured	Recapture Reproductive Condition
S	1	Male	25 Oct/72	SB	18 Mar/73	B++
T	1	"	4 Nov/72	NB	4 Jun/73	SB
U	1	"	Feb/73	SB	4 Jun/73	SB
V	1	"	21 Sep/72	NB	4 Jun/73	SB
W	1	Female	20 Mar/73	B	4 Jun/73	B
X	1	"	26 Mar/73	B	4 Jun/73	SB
Y	1	"	30 Mar/73	B	4 Jun/73	B
Z	1	"	6 Apr/73	B	4 Jun/73	SB

TABLE 10. *Taricha granulosa* ORIGINALLY CAPTURED IN BLINKHORN LAKE AND RECAPTURED ON LAND.

* = ANIMALS TAKEN FROM LAKE AND KEPT IN LAB UNTIL 2 OCTOBER, 1972, WHEN THEY WERE RETURNED TO LAKE.

\+ = ANIMALS TAKEN FROM LAKE AND PLACED ON LAND TO OVERWINTER.

++ = POSTREPRODUCTIVE.

Code	No.	Sex	Date of Original Capture	Original Reproductive Condition	Date recaptured	Recapture reproductive Condition	Direction of travel
A1	6	Male	4 Apr/72	B	late Oct/72	NB	to land*
A2	7	Female	4 Apr/72	B	late Oct/72	NB++	to land*
A3	2	"	18 Mar/73	B	18 Sep/73	NB++	to land
A4	2	"	21 Nov/72	NB	20 Sep/73	NB++	to land+
A5	1	"	18 Mar/72	B	16 Aug/73	NB++	to land
A6	1	"	2 Apr/72	B	16 Aug/73	NB++	to land*
A7	1	"	21 Nov/72	NB?	20 Mar/73	B	to lake+
A8	1	Male	4 Apr/72	B	12 Oct/73	NB	to land*
A9	1	"	4 Mar/73	B	14 Oct/73	NB	to land
A10	1	"	21 Nov/72	SB	26 Mar/73	SB	to lake
A11	1	"	2 Apr/72	B	7 Mar/73	SB	to lake
A12	1	"	21 Nov/72	NB?	20 Sep/73	NB	to land

TABLE 11. *Taricha granulosa* CAPTURED AND RECAPTURED ON LAND.

* = ANIMAL RELEASED IN LAKE.

Code	No.	Sex	Date of original Capture	Original reproductive Condition	Original direction of travel	Date recaptured	Recapture reproductive Condition	Recapture Direction of travel
B1	1	Male	11 Mar/73	NB	to lake	18 Sep/73	NB	to land
B1	1	"	18 Mar/73	NB	to lake	20 Sep/73	NB	to land
B2	2	"	late Oct/72	NB?	to land	7 Nov/72	NB	to lake
B3	1	"	21 Sep/72	NB?	to land	4 Nov/72	NB	to lake
B3	2	"	22 Sep/72	NB	*	late Oct/72	NB	to land
B4	1	"	20 Mar/73	NB	to lake	21 Mar/73	NB	to land
B5	1	"	4 Nov/72	NB	to land	19 Mar/73	NB	to lake
B6	19	Female	late Mar-early Apr/73	B	to lake	Mid Aug-Sep/73	NB	to land
B7	2	"	22 Sep/72	NB	*	23,28Oct/73	NB	to land
B8	5	"	12/14Mar/72	B	to lake	26/30Mar/73	B	to lake
B9	1	"	3 Mar/73	B	to lake	26 Mar/73	B	to land

may not have matured reproductively in 1973. One male migrant moving away from the lake in October, 1972 who returned to overwinter in water onemonth later (S, Table 8) was in breeding condition the following March. Males overwintering on land may not breed the following spring, as none in breeding condition were captured. Three male migrants who overwintered on land returned to the lake in nonbreeding condition the following spring (T - V, Table 9). All other males recaptured on land (B1 - B5, Table 11) were in nonbreeding condition.

Land-overwintered females can breed in consecutive years. Nine females (P, Q, Table 8; W, Y, Table 9; B8, Table 11) captured in spring 1972 and recaptured in spring 1973 were gravid both years. One postbreeding female who overwintered on land in 1972 was recaptured in breeding condition in spring of 1973 (A7, Table 10). Females who reproduce in the lake in spring and summer leave it as postreproductives before winter, apparently overwinter on land (A5, A6, Table 10), and may return to the lake to breed the following year. One such female was recaptured twice. She was taken as a postbreeder from the lake on November 19, 1972 (A4, Table 10) and placed on land, where she overwintered. She was taken gravid March 20, 1973 moving toward the breeding pond and was recaptured as a postreproductive moving away from the lake September 20, 1973 (B6, Table 11).

Most male migrants which were returned to the lake probably remained there, while female migrants taken to the lake did not. Of fifteen nonbreeding males and three nonbreeding females migrating away from the lake who were returned there, only two males (B3, Table 11) and two females (B7, Table 11) were recaptured moving in the original direction within a month. Three male migrants that left the lake were recaptured entering it within a month (B2, B3). All males and females were in nonbreeding condition on both occasions. The remaining female and thirteen males probably overwintered in the lake. One of the males was recaptured in the lake in breeding condition the following spring (S, Table 9).

Three females of five taken from the lake on November 21, 1972 and placed on land to overwinter (A4, A7, Table 10) were recaptured, and they bred in 1973. None of the five taken from the lake in fall 1972 and placed on land was recaptured returning to it in fall 1972. Of the 15 males taken from the lake in November, 1972 and placed on land none was recaptured. Thus females taken in fall 1972 from the lake to overwinter on land remained there, and females taken from the land and returned to the lake, were recaptured on land moving away from the lake within a month.

An extended egg-laying period is indicated by the recapture of females in the lake that were still gravid after at least ten weeks had elapsed (W - Z, Table 9). Two of these were thinner than before and had probably deposited several eggs by the recapture date (X, Z, Table 9).

Morphology and Histology

Female reproductive condition was initially assessed by external morphology. Large ovarian eggs produced a noticeable lateral body swelling. All females captured at the same time on land were in a similar reproductive stage. Of the few females taken on land in early winter (Table 2), all were in semibreeding condition both externally and internally. Eggs ranged in maximum size from just over half (1.03 mm) to 3/4 (1.49 mm) the diameter of matured eggs (1.92 mm).

Adult females taken on land moving toward the lake from late February to the end of the spring migration all contained a full complement of mature or nearly mature ovarial eggs, with a maximum diameter of 1.73 - 1.92 mm (Figs. 11, 12). All females taken on land at the end of the breeding season in late summer and early fall were slim, in nonbreeding condition, and upon dissection contained only small, immature, largely unpigmented eggs. Their ovaries also contained a few pigmented atretic eggs not deposited during the breeding season (Fig. 13). Postbreeding females weighed the least and had the smallest midoviduct diameters; females just prior to breeding weighed the most and had the largest midoviduct diameters.

On March 4, 1973, of thirteen (Table 4) lake-overwintered females the most mature individual was only in semibreeding condition (Fig. 14). The female with the smallest eggs resembled a postbreeder. Unhealthy or old females who overwinter in the lake also resembled postbreeders the following spring, and had small, undeveloped eggs. Larger eggs are more mature than smaller ones. Histological examinations of gonads indicated that external condition (presence or absence of lateral body swelling) and date of capture provided very reliable indicators of female reproductive condition.

Male primary sex character development follows. *Taricha granulosa* testis development is given in Table 12. Terms are defined in Appendix 8.

The testis, or lobe, matures anterior to posterior and is normally divided into two distinct parts, or lobules. The posterior lobule contains mature or maturing tissue used for reproduction the next breeding

FIGURE 11. A newly deposited *Taricha granulosa* egg showing the ovum, which is slightly oval, and jelly coats. Egg dimensions and jelly coat thicknesses are given.

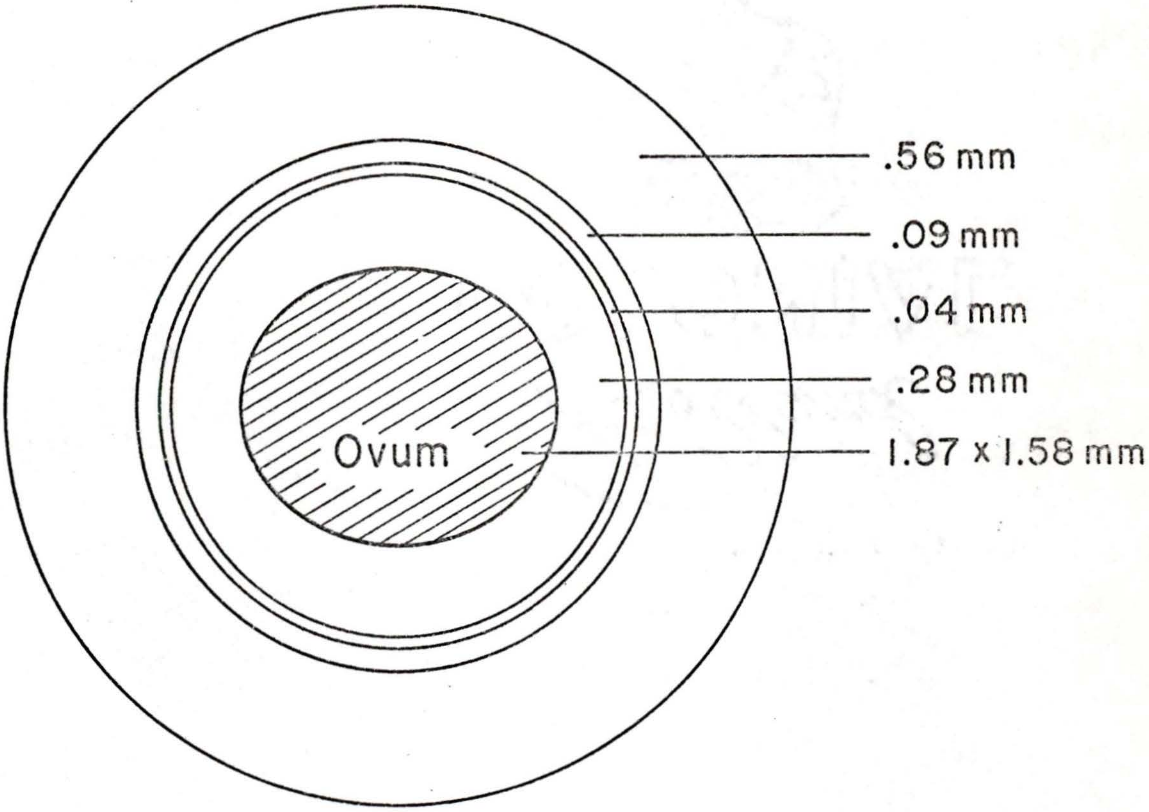

.56 mm
.09 mm
.04 mm
.28 mm
Ovum
1.87 x 1.58 mm

FIGURE 12. Mature eggs in ovary and two eggs (arrows) in oviduct. Land-overwintered female. Snout-vent length 5.5 cm., weight 7.53 grams.

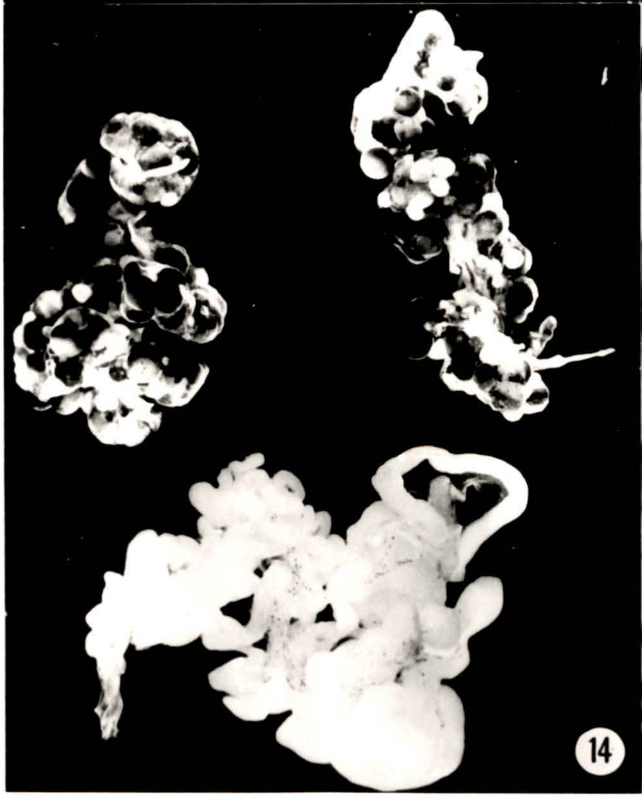
FIGURE 13. Degenerating pigmented eggs in ovaries of a postbreeding female (arrows). Captured on land moving away from water August 17, 1973. Snout-vent length 5.2 cm., weight 3.98 grams.

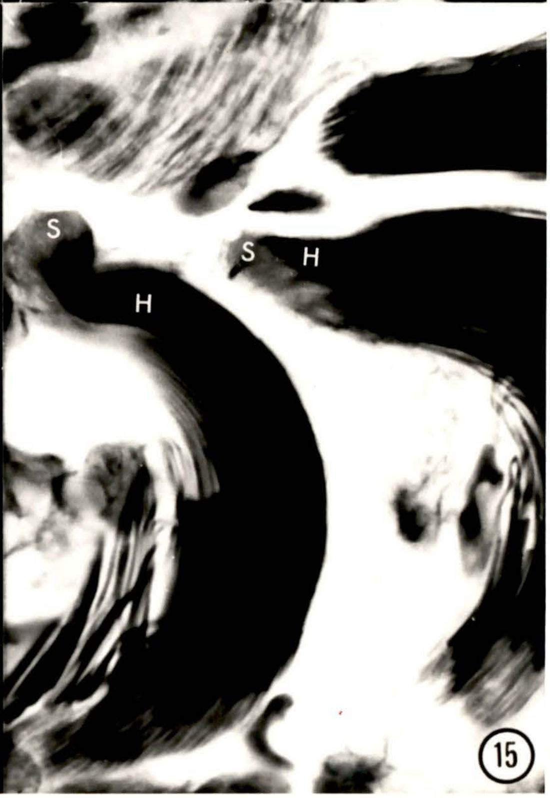
FIGURE 14. Mostly small, unmatured or maturing eggs and enlarging oviduct taken from a lake-overwintered female in Blinkhorn Lake March 4, 1973.

FIGURE 15. Two Sertoli cells (S) with sperm heads (H) attached. X 200


⑫


⑬


⑭



⑮

TABLE 12. TESTIS, WOLFFIAN DUCT AND SECONDARY SEXUAL CHARACTER DEVELOPMENT IN *Taricha granulosa* LAKE-OVERWINTERING MALES. ALL PERCENTAGES GIVEN ARE ± 5%.

Date	External Morphology*	Lobe configuration	Wolffian duct configuration
Oct-Dec	SB	50% to 75% maturing tubules, sperm formation, 50% - 25% spermatocytes	opening
Dec-Mid Jan	SB to B	75% maturing spermatids and sperm, 25% immature with spermatogonia and spermatocytes	open, few sperm, if any, present
mid Jan-April	B	75% mature with sperm and glandualr tissue 25% immature with spermatogonia and spermatocytes	open, initially packed with sperm to 30% full of sperm at end of breeding season
May	B to SB	75% to 25% degenerating glandular tissue, 25% to 75% regenerating tissue with spermatogonia and spermatocytes	sperm at end of breeding season 30% sperm in part of duct, part of duct degenerating
June	SB to NB	75% to 100% regenerating tissue with spermatogonia and spermatocytes	involuted
July-Sep	NB to SB	100% regenerating tissue, transition zone established	regenerating

* based upon secondary sexual characteristics.

season. The anterior lobule contains immature tissue used for breeding in two years' time. Young males have paired testes. Older males have a multiple testis of up to six lobes, three per side.

Male external morphology and date of capture were partial indicators of reproductive condition in nonbreeding males, and together with testis coloration provide an accurate index of male maturation. The light beige portion of a testis lobe contained active sperm or seminiferous tubules with recently evacuated sperm. Dark beige areas indicated the presence of regressing ampullae containing the glandular tissue of postreproductive animals. Ivory-gray areas contained spermatogonia and/or spermatocytes or spermatids that compose the maturing ampullae of prereproductive animals.

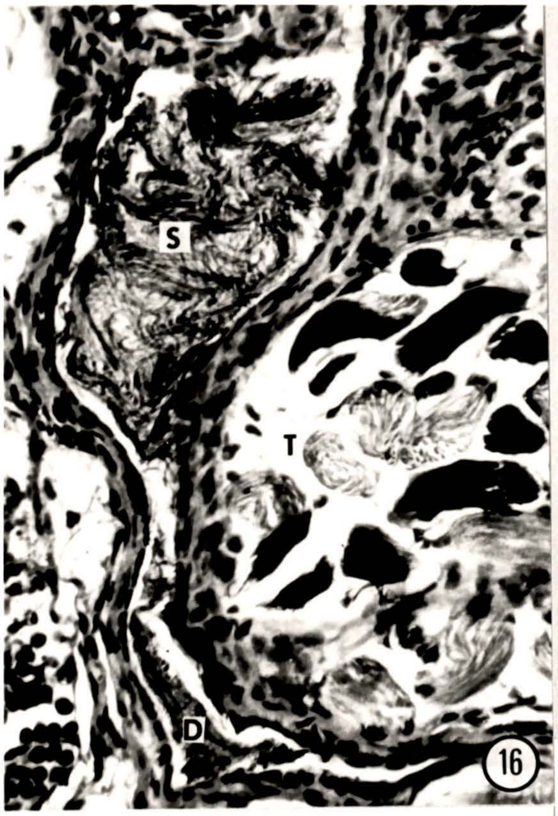
From October to December sperm were arranged in oriented bundles within the seminiferous tubules of prebreeding males' mature lobules. A Sertoli cell serves as the point of attachment for all the sperm heads in a group (Fig. 15). Sperm, just prior to evacuation from the seminiferous tubules in late winter and one to three weeks before copulation, become detached from the Sertoli cells. They become a disorganized mass and remain so as they travel from the tubule into an efferent duct (Fig. 16). Testis and mid sperm duct configuration in breeding males is given in Figures 17 - 19. After evacuation a few sperm may remain in the ampulla (Fig. 20). Sertoli cells apparently phagocytize the surplus sperm and other debris as they move toward the center of the tubule along the web-like connective tissue cytoplasm that engulfs the vacated area (Figs. 21 and 22). Eventually glandular tissue fills the entire postbreeding lobule (Fig. 23). This tissue

FIGURE 16. Ampulla with sperm (S) evacuating into an efferent duct (D). An adjacent tubule (T) still contains sperm.

FIGURE 17. Testis of a breeding male taken from Blinkhorn Lake March 18, 1973. Note glandular tissue (G) present in evacuated tubules. One band of sperm (S) 1 - 2 ampullae thick is not yet evacuated. Primary and secondary spermatocytes (C) fill the rest of the lobe. Snout-vent length 6.1 cm., weight 14.43 grams.

FIGURE 18. Testis of a breeding male taken from Blinkhorn Lake March 18, 1973. Sperm (S) and glandular tissue (G) present throughout most of the lobe. This animal had five lobes. A portion of a second lobe (L2) with the same configuration as the first (L1) is visible. Snout-vent length 5.6 cm., weight 9.64 grams.

FIGURE 19. Mid sperm duct of breeding male packed with sperm (arrows) just prior to spermatophore deposition. Same animal as in Figure 19.



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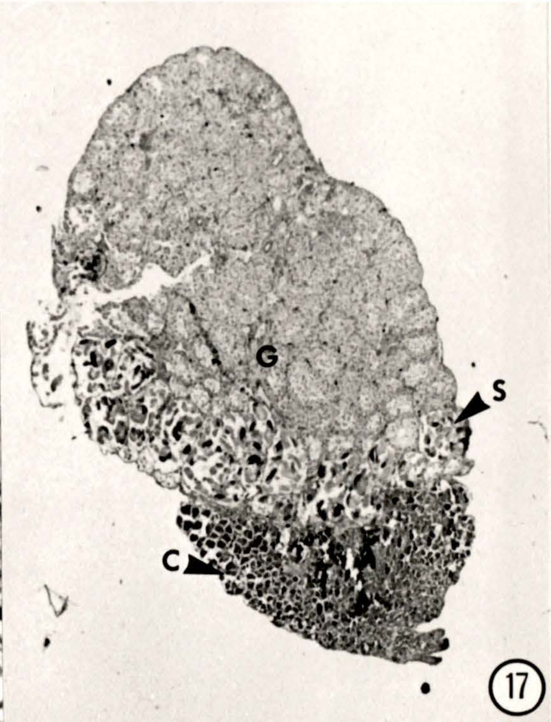

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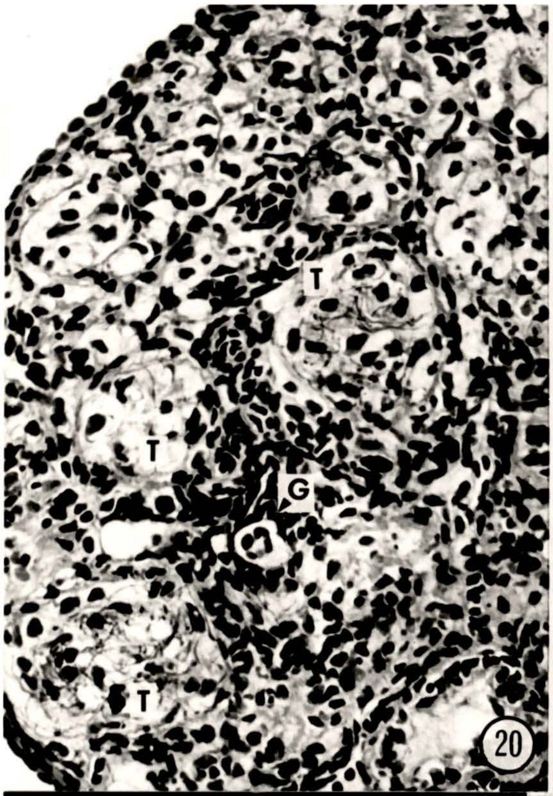
FIGURE 20. Recently evacuated tubules (T) with a few sperm remaining. A primary spermatogonium (G) with a lobed nucleus is visible among them.

FIGURE 21. Sertoli cells (arrows) phagocytizing sperms (S) remaining in a seminiferous tubule. No sperm remain in the periphery of the tubule on the top.

FIGURE 22. Sertoli cells (S) migrating along connective tissue cytoplasm (C) toward the center of a newly evacuated tubule. X 200

FIGURE 23. Glandular tissue in various stages of development; forming at the periphery (arrows) to well-developed (D) centrally.



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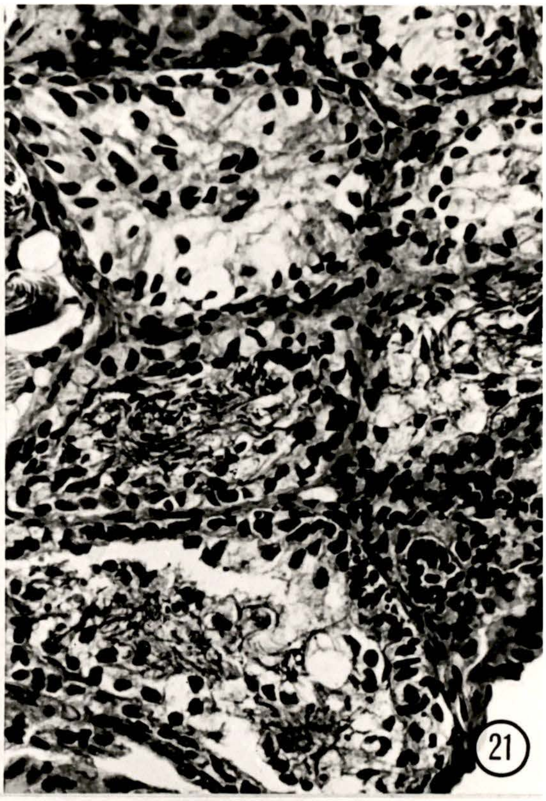

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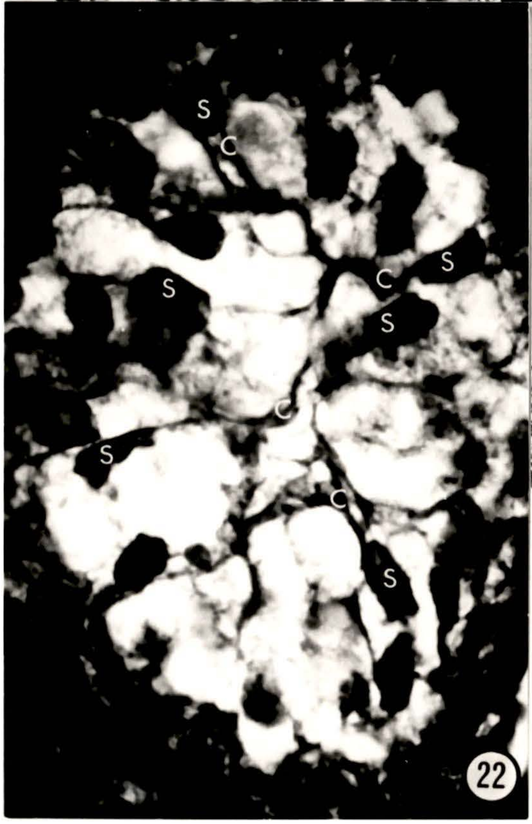

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begins degenerating while the sperm duct involutes from late April to mid May (Figs. 24 and 25), and is totally resorbed while the immature lobule enlarges as its once dormant sex cells begin dividing (Fig. 26). At this time a new lobe may form anterior to a constriction in the progonad (Figs. 27 - 29). A few primary spermatogonia may invade the testis itself from the cord during initial rapid lobe development (Fig. 30)

Each primary spermatogonium with a lobed, vesiculated nucleus (Fig. 31) produces secondary spermatogonia. Two secondary spermatogonia form the basis of the new seminiferous tubule (Fig. 32). Secondary spermatogonia multiply rapidly, giving rise to spermatocytes.

In early June the entire lobe of a postbreeding male contains primary and secondary spermatocytes and a few secondary spermatogonia, as the degenerating tissue of the once mature lobule has disappeared (Fig. 33). Primary spermatocytes, secondary spermatocytes, and spermatids may all be present within one seminiferous tubule (Fig. 34). The sperm duct is fully involuted at this time (Fig. 35).

The testis develops rapidly throughout summer and early fall. A transition zone of connective tissue (Figures 33 and 34) forms during this time, separating the lobe into what will become mature tissue the next breeding season from immature tissue that will develop in two years' time.

A few male lake-overwintered newts, old or unhealthy and emaciated, do not mature reproductively. They have almost translucent Wolffian ducts, indicating an absence of sperm and are half the weight of breeding males taken at the same time.

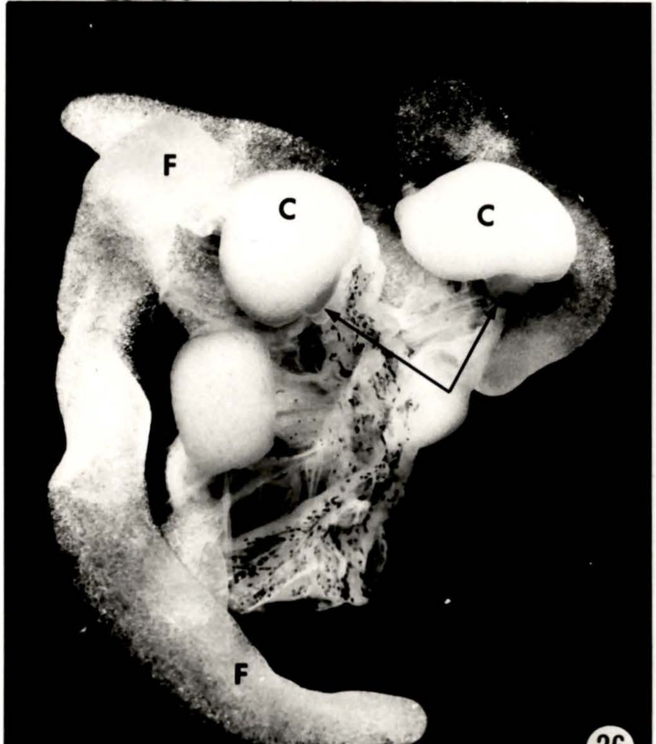
FIGURE 24. Degenerating glandular tissue (G) with maturing spermatocytes (S). May 3, 1973. Note primary spermatogonia (arrows) in the glandular tissue periphery.

FIGURE 25. Wolffian duct with a portion involuting and the remainder containing sperm (arrows) left over from the spring breeding season. Degenerating sperm are present in the involuting portions of the duct (I). Same animal as in figure 23.

FIGURE 26. Three-lobed newt testis taken from Blinkhorn Lake June 4, 1973. Note light-coloured, enlarged anterior portion of lobe containing spermatocytes (C); much shrunken, resorbing posterior portion of lobes (arrows). The fat body at this (F) time appears much enlarged and closely applied to the lobes. Snout-vent length 5.9 cm., weight 10.17 grams.


G
S
24


I
I
25


F
C
C
F
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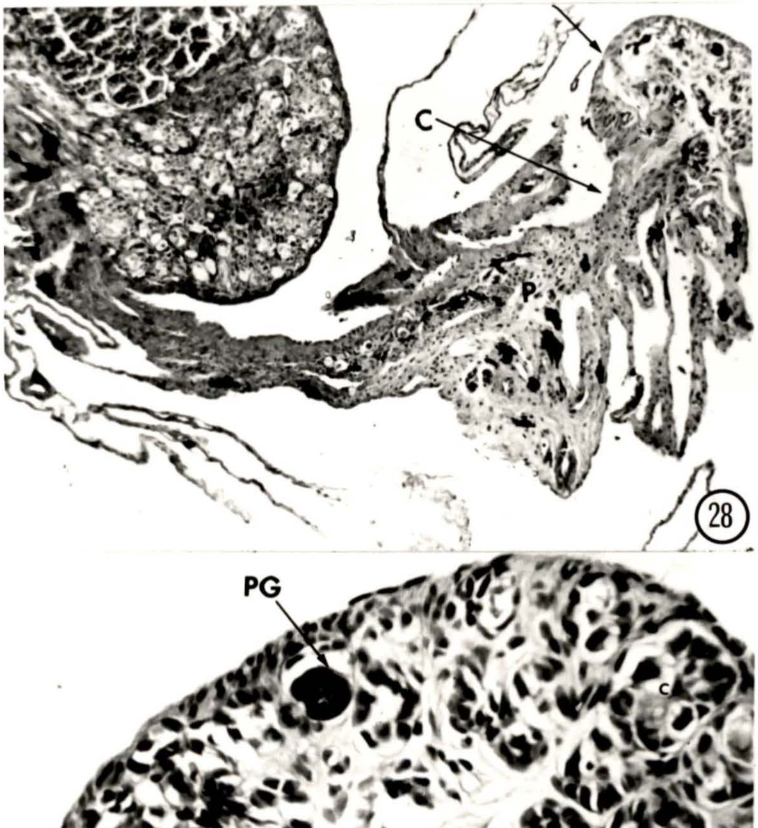
FIGURES 27, 28. A third lobe (arrow) is forming from a constriction (C) in the progonad (P). May 3, 1973. Snout-vent length 5.9 cm., 8.93 grams.

FIGURE 29. The newly forming testis lobe contains connective tissue (c) loosely arranged as in ducts. A primary spermatogonium (PG) with a lobed nucleus has invaded the developing tissue.


C
P
27

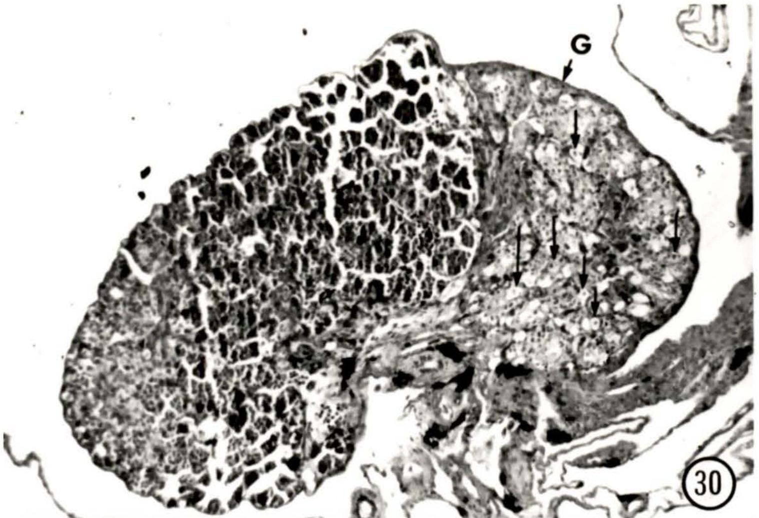

C
P
28


PG
c
c
29

FIGURE 30. Primary spermatogonia (arrows) present throughout the degenerating glandular tissue (G) of evacuated tubules.

FIGURE 31. Primary spermatogonia (P) with lobed, vesiculated nuclei in the cord of a postbreeding male.

FIGURE 32. Primary spermatogonia with lobed, vesiculated nuclei (N) in the cord of a postbreeding male. Several secondary spermatogonia (SG) are also present. Two secondary spermatogonia (arrow) in one ampulla are dividing, and these will eventually form a mature seminiferous tubule.



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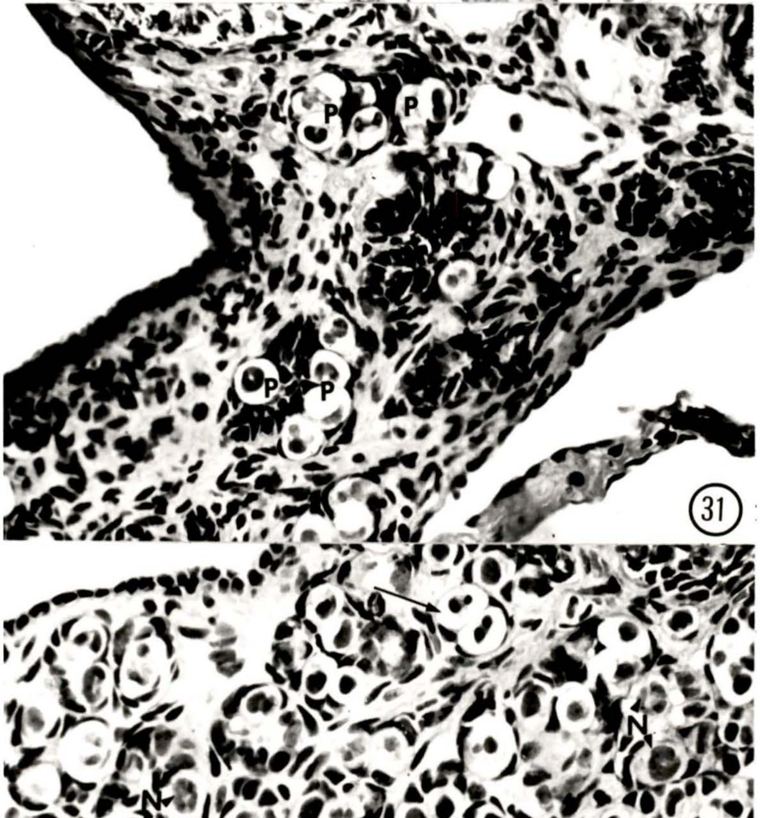

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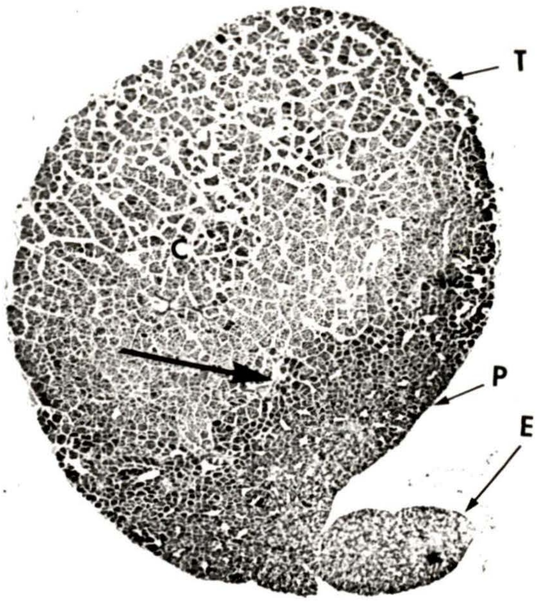
FIGURE 33. Regenerating, maturing testis. Postbreeding male. The transition zone (arrow) of connective tissue has just begun to form between the area with secondary spermatocytes and spermatids (T), and the area with primary and secondary spermatocytes (P). The former will mature into sperm by the following spring. The latter will stop maturing once the transition zone is complete and serve as the breeding stock in two years' time. The epigonad (E) with primary spermatogonia is also visible. June 4, 1973. Snout-vent length 5.9 cm., weight 10.17 grams.

FIGURE 34. Seminiferous tubules with spermatids, primary and secondary spermatocytes, all of which may be contained within one ampulla (outlined A). A portion of the developing transition zone (arrow) is visible. Same animal as in figure 32.

FIGURE 35. The involuting mid sperm duct of a postbreeding male. Fluid and degenerating sperm (arrows) fill intercellular spaces. Same animal as in figures 33 and 34. Compare to open, mature duct in figure 19.



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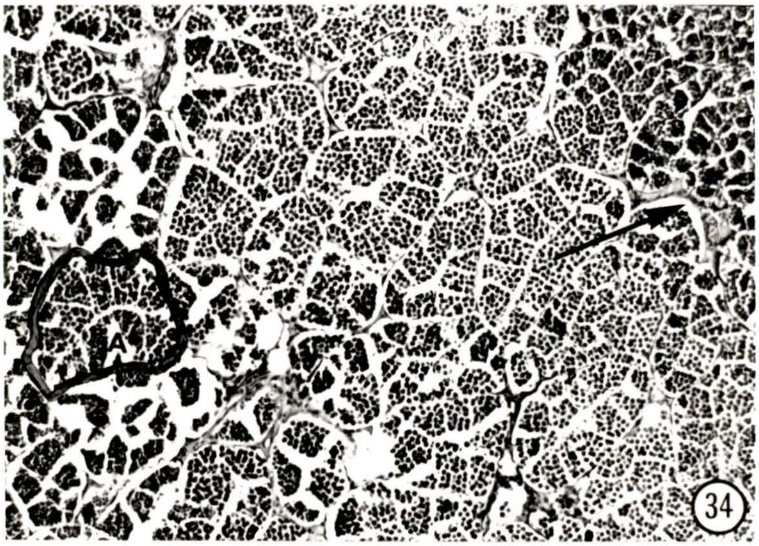

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About one-third of the males captured on land returning to the breeding pond in spring 1973 were small and in nonbreeding condition. The efferent ducts and sperm duct was thick-walled and occluded (Fig. 37), preventing any sperm from being used for fertilization. This indicated that these animals were first year adults. Contrast figure 37 to the open duct of mature males (Fig. 19). The testis (Fig. 36) was approximately 20% mature and packed with sperm. Sertoli cells were actively phagocytizing the sperm, which appeared healthy. Healthy sperm notably had tails that stain a much darker red just behind, and a lighter red, posterior to the heads. Unhealthy, degenerating sperm tails stained pale red with eosin throughout. Efferent ducts, closed when unhealthy sperm were present, were open when healthy sperm were present.

Thirteen of fifteen 1972 - 1973 land-overwintered males examined were second year or older adults who bred at least once before and thus had open ducts. None matured to the extent that lake-overwintered males did. The land-overwintered male with the largest percentage of mature tissue (Fig. 38 cf. Fig. 18) was in semibreeding condition externally. His sperm duct contained few sperm (Fig. 39 cf. Fig. 19). He probably left the lake in fall, reentered the lake in February before females, then matured somewhat in water. The presence of newly-formed glandular tissue in males who probably overwintered on land and returned to the lake in February indicated that sperm were evacuated from their lobes two to four weeks after those of lake-overwintered males, whose glandular tissue was fully formed in March.

About half of the land-Overwintered males showed a testis config-

36. Testis of a first year adult male with 20% mature tissue (arrow). Several ampullae are devoid of sperm (A). Sertoli cells have removed them from this area. March 28, 1973. Snout-vent length 5.3 cm., weight 5.90 grams.

FIGURE 37. The closed, thick-walled Wolffian duct of a first year adult male. Same animal as in figure 35.

38. Testes of a land-overwintered male taken in Blinkhorn Lake. Sperm are present, evacuating, or have just been evacuated from all mature seminiferous tubules. Snout-vent length 5.5 cm., weight 6.07 grams.

FIGURE 39. Sperm duct nearly half full of mature sperm (S). Same animal as in figure 38. March 4, 1973.

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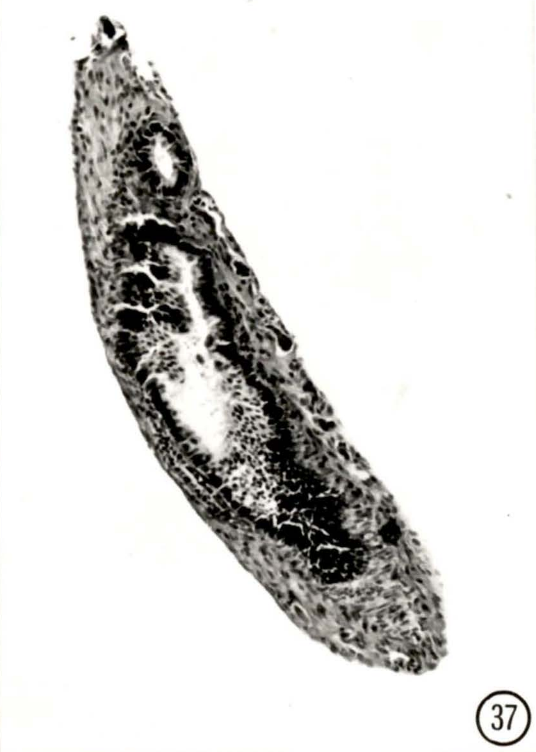

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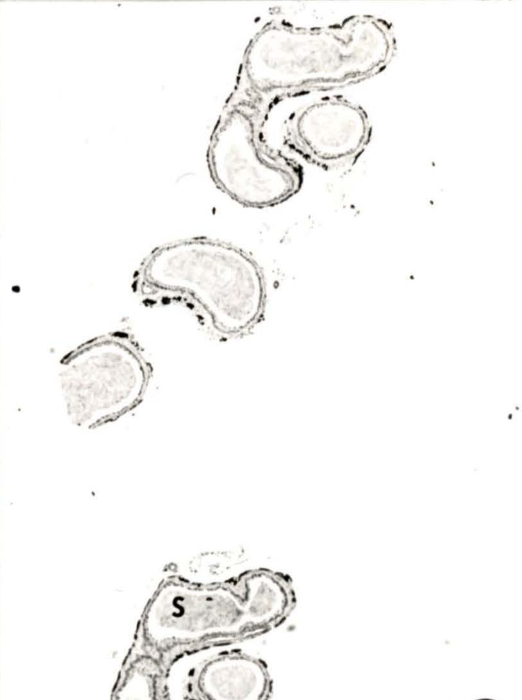

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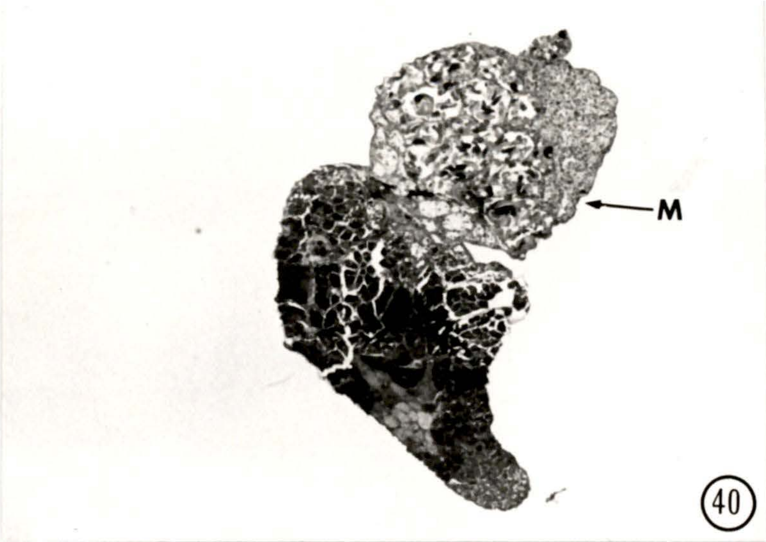
FIGURE 40. This testis is almost half mature (M). April 8, 1973. Snout-vent length 6.3 cm., weight 8.47 grams.

FIGURE 41. This testis is about one-third mature. May 22, 1973. Snout-vent length 5.6 cm., weight 9.02 grams.

FIGURE 42. The sperm duct shows thickened duct walls (arrows). Compare to figure 19.



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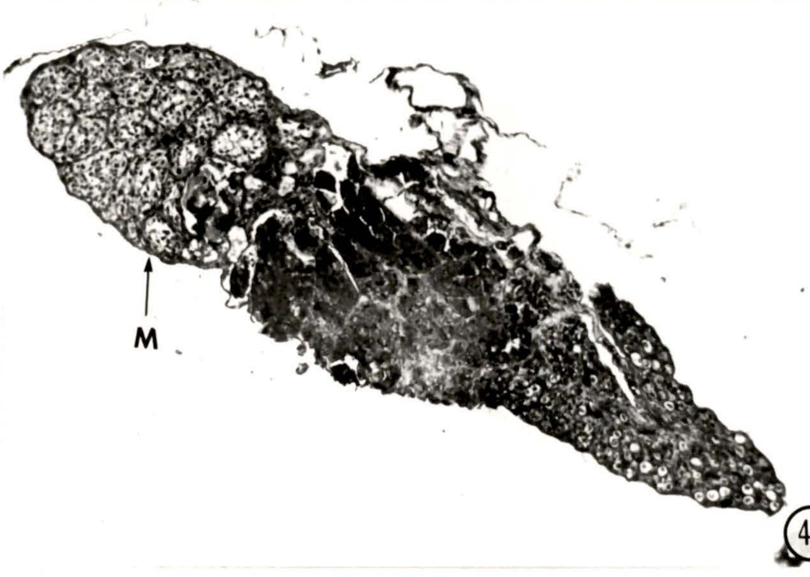

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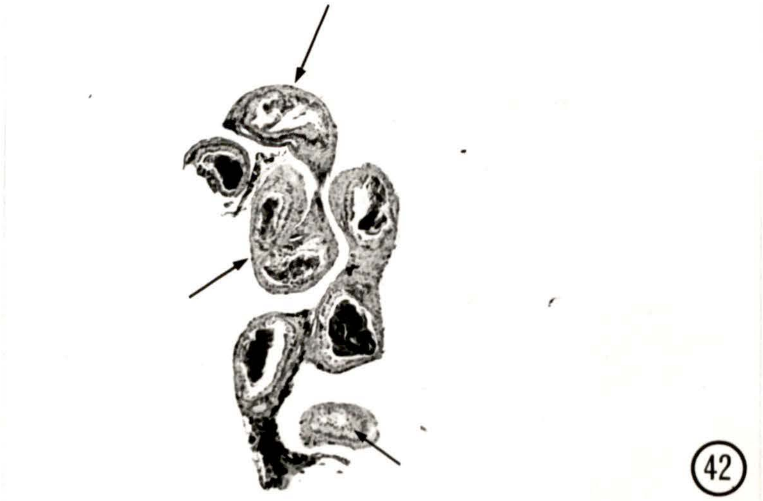

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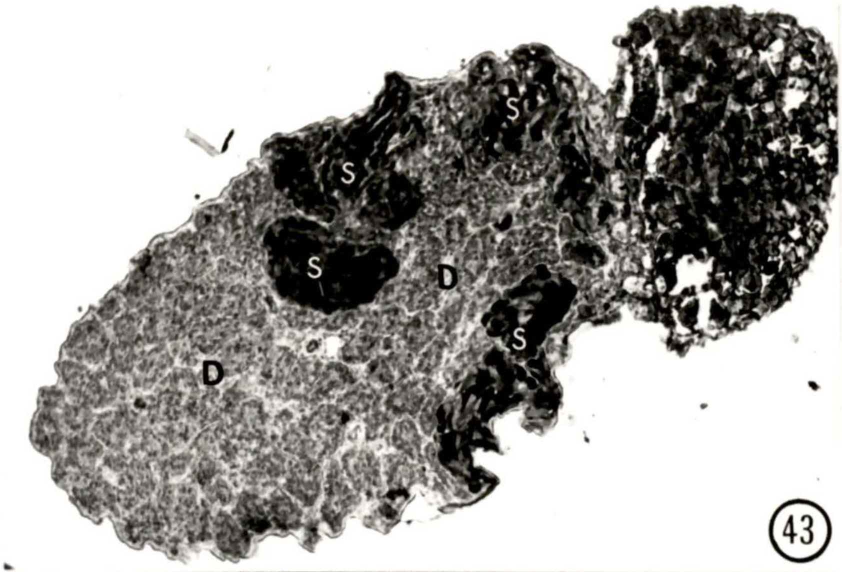
FIGURE 43. Most of this lobe is degenerating. Sertoli cells have begun to destroy remaining sperm (S) and are degenerating where no sperm remain (D). Same animal as figures 44, 45.

FIGURE 44. Sertoli cells (arrows) are seen phagocytizing sperm at the sperm mass border. Detail of figure 43.

FIGURE 45. Most sperm in this area have already disappeared. Detail of figure 43.



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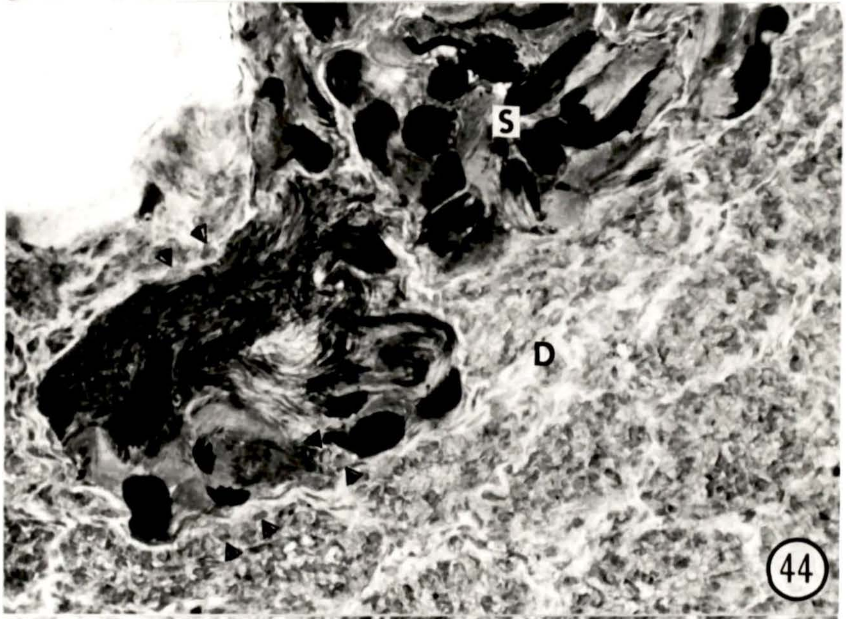

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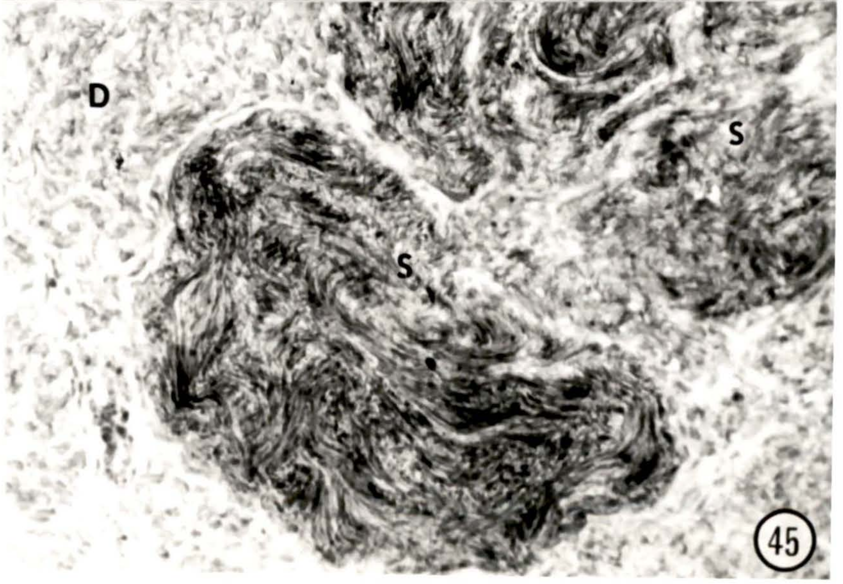

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uration in which lobes were partly degenerating or had smaller proportions of matured tissue than breeding, lake-overwintered males (Figs. 40 - 45, Table 13 cf. Table 12). There was a tendency for older land-overwintered males to develop more mature tissue than younger animals (Table 13). By contrast, males overwintering in the lake showed no apparent difference in their extent of maturation.

An extreme example of the effects of land overwintering is shown in Figures 46 and 47. This otherwise healthy animal was in nonbreeding condition externally and had two testis lobes. The entire testis is beginning to degenerate. The cord, however, contains primary spermatogonia apparently capable of later replacing the degenerating tissue. The sperm duct contains sperm left over from the previous year that are also degenerating (Fig. 48). Spermatogenesis did not progress beyond the spermatocyte stage.

TABLE 13. TESTIS MATURATION IN *Taricha granulosa* LAND-OVERWINTERED MALES.

Total no. lobes	% mature tissue (range)	mean % mature tissue	no. lobes examined
2	0 - 40	17.5	12
3	10 - 30	20	3
4	20 - 50	40	8
5	30 - 50	40	8
6	30 - 50	42.5	8

FIGURE 46. Degenerating lobe of an adult land-overwintered male. A portion of the epigonad (E) with primary spermatogonia is visible. Captured on land March 28, 1973.

FIGURE 47. Degenerating primary spermatocytes (D) of an adult land-overwintered male. Same animal as in figure 46.

FIGURE 48. Mid sperm duct showing degenerating sperm (D) from the 1972 breeding season. Same animal as in figures 46 and 47.

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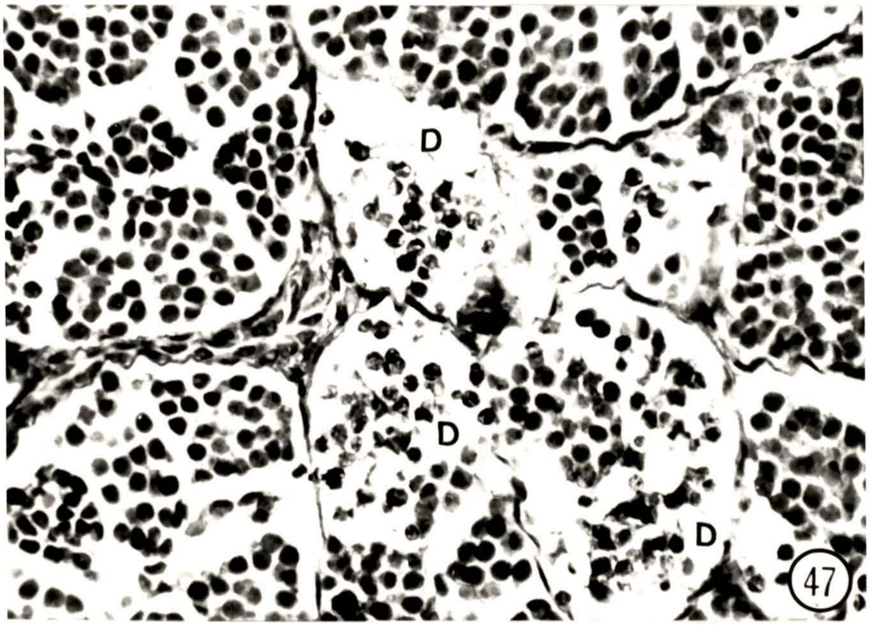

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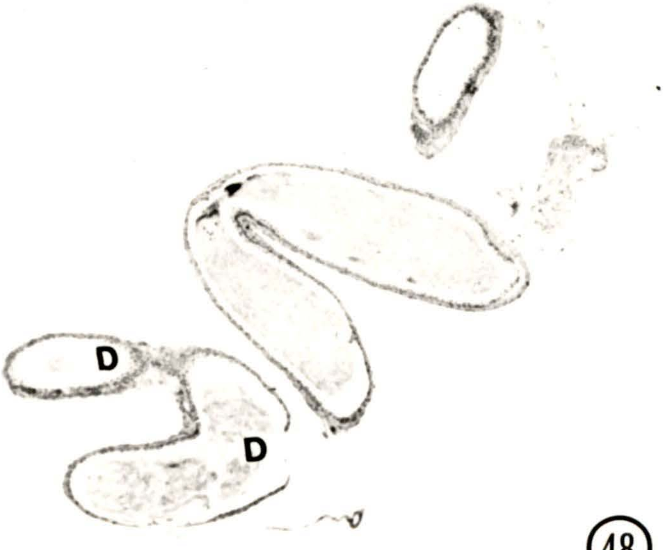

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DISCUSSION

The in situ observations, trap records, and recapture data indicates *Taricha granulosa* at Blinkhorn Lake on Southern Vancouver Island exhibits sexually dimorphic overwintering behaviour and that normal reproductive development is closely associated to the overwintering habitat. Adult males are usually aquatic throughout the year. Females and juveniles of both sexes overwinter on land. Recapture data of some newts indicate most adults probably breed in consecutive years. Histological examiniations, however, show that males overwintering on land and females overwintering in water do not fully mature the following breeding season.

Newts of some other genera, by contrast, remain permanently aquatic like *T. granulosa* males when permanent ponds are available. For example, adults of *Notophthalmus viridescens*, the red-spotted newt of eastern North America, are active all year in permanent ponds (Neill, 1948; Chadwick, 1944; Collins, 1932) or in water near breeding ponds (Cagle and Smith, 1939) that contain a rich flora (Noble, 1926). Pond populations may comprise 68 - 86% males (Collins and Fencil, 1932). Aquatic newts remain active all winter, and occasionally move onto stream banks within ten feet of water (Morgan and Grierson, 1932) but burrow into the mud during cold weather (Bishop, 1941). Eurasian *Triturus* adults generally overwinter on land, although some species overwinter in water. *T. marmoratus* moves in and out of water throughout the year, *T. montandoni* is terrestrial in summer only, while some *T. cristatus* populations are permanently aquatic (Steward, 1966). *Cynops* *orientalis*, a Chinese species, is permanently aquatic (Chang and Boring, 1935).

Previously, there has been only one study covering a full seasonal cycle in a permanent pond situation (Ritter, 1897). It showed that *T. torosa* males are permanently aquatic while females are terrestrial during the nonbreeding season.

Several authors have suggested that *Taricha granulosa* adult males would remain entirely aquatic in parts of the range not prone to flooding or seasonal drought (Pimentel, 1960; Riemer, 1958; Twitty, 1942). However the results of studies in permanent ponds in Oregon (Coates et al, 1970; Chandler, 1918) and on the British Columbia mainland (Neish, 1970; Efford and Mathias, 1969; Mathias, 1964) suggested that males are not aquatic in winter. However the conclusions these authors reached are in question, since overwintering lake animals are extremely difficult to find. For example, divers employed in the present study found no newts during a half hour search until instructed how and where to look for them. When told that leopard frogs in Ontario wintered submerged in silt in the mud bottom of an ice-covered lake (Emery et al, 1972) and painted turtles wintered in the mud in Pennsylvania ponds (Ernst, 1972) they recovered twenty-four newts from the mud within the next half-hour. Consequently in winter the pond mud habitat should be more thoroughly examined in future studies.

Physiological evidence also exists to support newt lake overwintering. At 5°C. *T. granulosa* can meet 87.3% of its oxygen demand by uptake from water through the skin (Coates, 1970/1971). At 15°C.

only 50% of its oxygen demand can be obtained through the skin (Whitford and Hutchinson, 1965). Thus newts may remain submerged in mud and undetected indefinitely in fall and winter when water temperatures are low, but are easily seen in spring and summer when they surface to breathe.

Obviously permanent pond residence cannot occur where ponds are temporary. In such cases *Notophthalmus viridescens* is forced to move to moist areas on land when ponds dry up (Pope, 1924; Gage, 1891) and its smooth adult skin typical of aquatic newts changes to a rough terrestrial form when adults move onto land (Jopson, 1936). Similarly, *Taricha torosa* and *T. granulosa* habitat is temporary water, except on the northwest coastal areas of Washington, British Columbia, and Alaska. Few studies have been done in this northern part of the range and none have continued through the winter. Consequently *T. torosa* and *T. granulosa* males are possibly incorrectly characterized as terrestrial during the nonbreeding season (Neish, 1970; Efford and Mathias, 1969; Pimentel, 1960; Riemer, 1958; Storer, 1925; Chandler, 1918) and would probably remain aquatic if permanent ponds were available. *T. rivularis*, the remaining member of the *Taricha* genus, is probably unique in being terrestrial during the nonbreeding season even where permanent water is available (Twitty, 1966).

Female nonbreeding habitat varies among newt genera. Generally females are more terrestrial than males even when permanent ponds are available. *Triturus* females are mostly terrestrial during the nonbreeding season (Steward, 1969; Creed, 1964). *Tylototriton verrucosus* is terrestrial from October to March (Pope, 1931). Most

Notophthalmus viridescens remain aquatic in permanent ponds (Bishop, 1943) although some are probably terrestrial in fall and early spring (Collins and Fencil, 1932) or in summer in different parts of its range (Hurlbert, 1969). Female *Taricha granulosa*, like other *Taricha* (Twitty, 1959; Stebbins, 1954b; Miller and Robbins, 1954), move to land as postreproductives and remain terrestrial until they migrate to the same breeding pond one or two seasons later, normally during or just after a rainfall.

Some irregularities in the apparently normal *T. granulosa* overwintering pattern were observed during the study. In 1972 some males from Blinkhorn Lake were observed on land for the first time. Although male migration from water to land was not observed in the study area in 1970 and 1971, it may have occurred on a small scale and gone unnoticed. Pimentel (1960) reported that *T. granulosa* males in Oregon displayed a marked tendency to repeatedly move in and out of ponds. Evidence that at least some males spent only a short time on land and then returned to the lake in fall 1972 is indicated by recapture of three marked males returning to the lake (Table 11, B2, B3). Freezing weather and a one-month drought may have prevented more males from returning to the lake.

In this study, evidence that *T. granulosa* males wintering in ponds and females wintering on land probably breed in consecutive years was derived from recapture records. Efford and Mathias (1969) reported that 72% of the breeding animals taken in one year from Marion Lake, British Columbia, were recaptured the next and concluded that most *T. granulosa* breed in consecutive years. The low recapture rate in Blinkhorn Lake may reflect low trapping success, although females in large numbers possibly left the lake when traps were not in place during unusually high rainfall in July, 1972. It is unlikely that female newts used different breeding ponds in different years. Twitty (1966) demonstrated a high degree of fidelity to the home breeding area. Alternatively, some individuals may not breed in successive years, and would not be expected to return to the breeding pond in non-breeding years.

In 1970 and 1971, old or unhealthy females (emaciated with vertebrae and girdles protruding through the skin) did not migrate but remained in Blinkhorn Lake. Recaptures showed that they were not in breeding condition the next year. Histologic analysis showed that healthy pond-overwintered females in fall and winter of 1972-1973 also did not fully mature by spring, 1973. By contrast healthy land-overwintered females possessed fully mature gonads in 1973. Similarly 1972 lake-overwintered males fully matured reproductively in 1973 while land-overwintered males did not. One male who spent only a short time on land and returned to the lake to overwinter was in breeding condition the following spring (Table 9, S). These data are in agreement with Adams' (1940) statement that male *Notophthalmus* may require a prebreeding aquatic period to fully mature.

Land-overwintered males returning to the lake in 1973 mostly lacked secondary sex characters. The testes were degenerating in some. Similarly testes of land-overwintered first year adult males contained only 20% mature, degenerating tissue while lake-overwintered male testes contained 75 - 80% mature, healthy tissue. The single male migrant captured in March, 1972 (Table 2) was probably a first year adult male. It thus seems that complete gonadal maturation in male *T. granulosa* is related to the choice of an aquatic, nonbreeding overwintering habitat. The reason that older land-overwintered males came closer to sexual maturity than younger ones (Table 13) is unknown.

Certain other aspects of the Taricha granulosa reproductive cycle are important. For example the breeding season in permanent ponds may be at least twice as long as in temporary pond situations. While long breeding seasons are dependent on the availability of permanent or near permanent water, its biological significance is probably related to climate. Low winter temperatures precede summer drought in parts of coastal Europe and North America, apparently often severely limiting the length of the breeding season and thus newt reproductive success (Porter, 1972; Steward, 1969; Jopson, 1936; Pope, 1924). Zweifel (1968) noted that drought may severely limit amphibian recruitment where animals breed in temporary bodies of water. Balinsky (1969) found frog recruitment diminished first by cold early in the season and later by drought in South Africa. Studies on amphibian thermal requirements (Brattstrom, 1963) indicate that urodeles are generally more stenothermal than anurans, hence their embryos are probably very susceptible to unseasonal cold snaps. See Table 14.

The results of the present study suggest that optimization of breeding success of *T. granulosa* is dependent on a variety of adaptations including: early male breeding readiness, the use of spermatophores for fertilization, female breeding readiness, discontinuous egg deposition, and possibly synchronous egg laying.

TABLE 14. LENGTH OF NEWT BREEDING SEASON FROM MALE WATER ENTRANCE OR SECONDARY SEX CHARACTER DEVELOPMENT TO THE END OF EGG DEPOSITION

Species	Breeding Habitat	Breeding Season Length	Reference
Notophthalmus viridescens	temporary ponds	≃5 months	Brimley, 1921
Notophthalmus viridescens	permanent ponds	9 months	Bishop, 1941
Triturus spp.	temporary ponds	1-2 months	Creed, 1964
Triturus spp.	permanent ponds	3 months	Steward, 1969
*Pleurodeles waltl**	permanent ponds	9 months	Steward, 1969
Tylototriton verrucosus	permanent ponds	≃3 months	Pope, 1931
Taricha rivularis	temporary streams	1½ months	Twitty, 1966
Taricha torosa	temporary streams	2 months	Miller and Robbins, 1954
Taricha torosa	temporary ponds	2½ months	Miller and Robbins, 1954
Taricha torosa	permanent ponds	6½ months	Ritter, 1897
Taricha granulosa	temporary ponds	4 months	Pimentel, 1960
Taricha granulosa	permanent ponds	6½ months	Chandler, 1918
Taricha granulosa	permanent pond	6½ months	this study

* The Iberian newt may breed at almost any time of year.

The reproductive advantage of early male breeding readiness was evident in Blinkhorn Lake in 1971 and 1973 when a mild and rainy winter was followed by a dry summer. Male *T. granulosa* in the lake were ready to breed in January of 1973 as indicated by large numbers of amplecting homosexual male pairs in breeding condition. Such early male maturation has been noted elsewhere (Oliver and McCurdy, 1974; Hurlbert, 1969; Smith, 1941). European *Triturus* and mainland *Taricha* males are generally in breeding readiness about one month before females arrive (Steward, 1969; Pimentel, 1960; Storer, 1925; Chandler, 1918). In 1973 Blinkhorn Lake females began arriving in January, two months earlier than the normal mid March peak migration period. Later that same spring about half of Blinkhorn Lake's surface area became dry land (air photo, Figure 4). With this combination of climatic conditions the eggs of early female migrants fertilized by early maturing males probably survived best whereas eggs laid late in the season in typically shallow water locations probably died.

An extended female breeding season is made possible partly as a result of spermatophores, or sperm packets, produced by males, and deposited in the cloaca during courtship (Davis and Twitty, 1964). Once a supply of sperm is secured breeding males have completed their contribution to the year's production. Salamander sperm may remain viable in spermathecae for six months or more (Sayler, 1966; Blanchard, 1934). Eggs are fertilized internally as they pass from the oviduct through the cloaca. One spermatophore may serve to fertilize the entire egg production of one season. In Blinkhorn Lake males become reproductively inactive beginning two months before egg deposition ends.

An extended female breeding season would increase the chances of reproductive success in the context of unpredictable climatic changes; for example if a late frost follows a mild period when eggs are deposited, eggs laid later in the season after danger from low temperatures is past would survive. Balinsky (1969) found cold a major factor limiting amphibian recruitment.

In Blinkhorn Lake individual females probably deposit eggs over a four month period. Eggs are laid individually, probably several in succession over a period of a few days followed by a non-laying period of up to a few weeks. Such discontinuous egg deposition may underlie the extended breeding season in *T. granulosa* females. In a species of relatively low fecundity it has the additional advantage of increasing the chances that progeny of individual females will survive despite unpredictable climatic changes.

Collections of eggs from Blinkhorn Lake did not show a continuum of developmental stages but rather different groups of eggs at different stages of development. Besides confirming discontinuous egg deposition, the observation suggests some form of synchrony among females in egg deposition. Neither the initiating factors, behavioural or environmental, nor the biological significance of this synchrony is understood.

The histological evidence of this study shows that the reproductive development of *T. granulosa* is similar to that described for other Salamandridae, including *Notophthalmus viridescens* (Adams, 1940), *Triturus* (de Beaumont, 1929; Aron, 1924), *Euproctus* (Rouy, 1972) and *Taricha torosa* (Miller and Robbins, 1954; McCurdy, 1931). One major difference between spermatogenesis in *T. granulosa* and other Salamandrid spermatogenesis is that cells from the mesonephrogenic cord migrate into the gonad during rapid testicular development after breeding ceases. This was previously reported only in *Euproctus* larvae (Rouy, 1970). The retention of lobed, vesiculated nuclei in primary spermatogonia after they disappear from the embryonic epidermis is related to rapid gonadal development.

The major finding of this study was that male *T. granulosa* on southern Vancouver Island normally remain permanently aquatic, while females are terrestrial during the nonbreeding season. Histologic analysis shows that animals which follow the above pattern can reproduce the following breeding season, while the reproductive capacity of the few land-overwintered males and lake-overwintered females is impaired.

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APPENDIX 1. BLINKHORN LAKE WATERSHED AND MORPHOMETRIC CHARACTERISTICS

longitude	48° 23' 30" N.
latitude	123° 34' 30" W.
elevation	425 feet
land drainage area	93 acres
land drainage area/lake surface area	16.96
land use	95% forested, 5% settled (Dense woodland to scrub grassland[1]). Old logging road borders entire eastern side of lake and cuts across drainage inflow from Mt. Blinkhorn; Kangaroo Road cuts across southern end of basin
vegetation	primarily coniferous forest, some swamp land
surface materials	rough-mountainous - thinly mantled
geology	olivine gabbro[2]
drainage system	open
inlet	seasonal, off Mt. Blinkhorn
outlet	seasonal, to west by seepage and seasonal flow, possibly to Veitch Creek, Hutchinson Cove, and Sooke Basin
maximum length	706 feet
maximum width	413 feet
mean width	339 feet
maximum depth	19.4 feet
mean depth	8.5 feet
mean depth/maximum depth	.44
direction of major axis	N - S, 30°E. of magnetic N.
lake surface area	5.5 acres or 239,602 square feet
number of islands	none
shoreline length	1852 feet
volume	46.6 acre-feet or 2,031,721 cubic feet
mean slope of lake bottom	8.19%

[1] Forward, 1969

[2] Clapp, 1917

APPENDIX 2. BLINKHORN LAKE AREA AND VOLUME CHARACTERISTICS

Depth ft.	Area acres		Area sq. ft.	% Total Surface Area
0(s)	5.501		239,602.3	100.00
3	4.669		203,401.6	84.89
6	3.576		155,778.9	65.02
9	2.623		114,251.4	47.68
12	1.263		54,994.9	22.95
15	0.691		30,083.5	12.56
18 (18.8 max.)	0.055	0.146	2,390.0	1.00
18 (19.4 max.)	0.091		3,945.4	1.65

Stratum ft.	Acres ft.	Volume cu. ft.	% Total Volume	Cumulative % Volume
0 - 3	15.238	663,965.07	32.68	32.68
3 - 6	12.322	536,906.26	26.43	59.11
6 - 9	9.262	403,572.94	19.86	78.97
9 - 12	5.706	248,627.42	12.24	91.21
12 - 15	2.888	125,838.77	6.19	97.40
15 - 16	1.155	50,326.79	2.48	99.98
18 - 18.8	0.015	653.59	0.03	99.91
18 - 19.4	0.042	1,830.07	0.09	100.00
TOTAL	46.628			

APPENDIX 3. BLINKHORN LAKE AQUATIC VEGETATION[1], AUGUST, 1970

SCALE + (RARE) TO 5 (ABUNDANT).

Shore to water 5 cm deep.
Herb layer height 100 cm.
No moss layer. 100% cover.

Carex sitchensis	5
Lycopus uniflorus	1
Comarum palustre = *Potentilla palustris*	1
Veronica scutellata	1
Epilobium cf. watsonii	+
Galium trifidum	+
Nuphar polysepalum	+
Juncus acuminatus	+
Mentha arvensis	+
Myosotis laxa	+
Hypericum anagalloides	+
Spirea douglasii	+

Herb layer height 190 cm. 100% cover.
No moss layer. Water 5 to 15 cm. deep.

Scirpus validus	5
Nuphar polysepalum	2
Carex sitchensis	+
Lycopus uniflorus	1
Veronica scutellata	+
Typha latifolia	+

Water 15 to 80 cm. deep
80% cover.

Sparganium minimum	3
Utricularia vulgaris	2
Elodea canadensis	1
Chara sp.	2
Potamogeton berchtoldii	1
Ceratophyllum demersum	+
Potamogeton gramineus	+

Water 80 to 130 cm. deep.
Floating 30%
Submerged 100%

Nuphar polysepalum	3
Chara sp.	3
Elodea canadensis	2
Sparganium minimum	2
Utricularia vulgaris	2
Potamogeton berchtoldii	+
Ceratophyllum demersum	+

In deeper water: colonies of *Potamogeton amplifolius*, colonies of artifically planted *Nymphaea*, 2 spp., and large colonies of *Ceratophyllum demersum* to a depth of 10 - 12 feet. Center of lake is void of vegetation - lake bottom covered with a flocculent mud.

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[1] after Braun-Blanquet, 1932.

APPENDIX 4. DOMINANT TERRESTRIAL VEGETATION IN THE BLINKHORN LAKE WATERSHED.

Lake Border		Upland Watershed
Alder (*Alnus rubra*) Willow (*Salix spp.*) Red Cedar (*Thuja plicata*)	Trees	Western Hemlock (*Tsuga heterophylla*) Douglas Fir (*Pseudotsuga menziesii*) Red Cedar (*Thuja plicata*)
Spirea (*Spirea douglassi*)	Shrubs	Salal (*Gaultheria shallon*)
Sedge (*Carex sitchensis*) Reed (*Scirpus validus*)	Herbs	sparse, patchy
sparse, patchy	Moss	sparse, patchy

APPENDIX 5. LAND AND WATER TEMPERATURES AT BLINKHORN LAKE

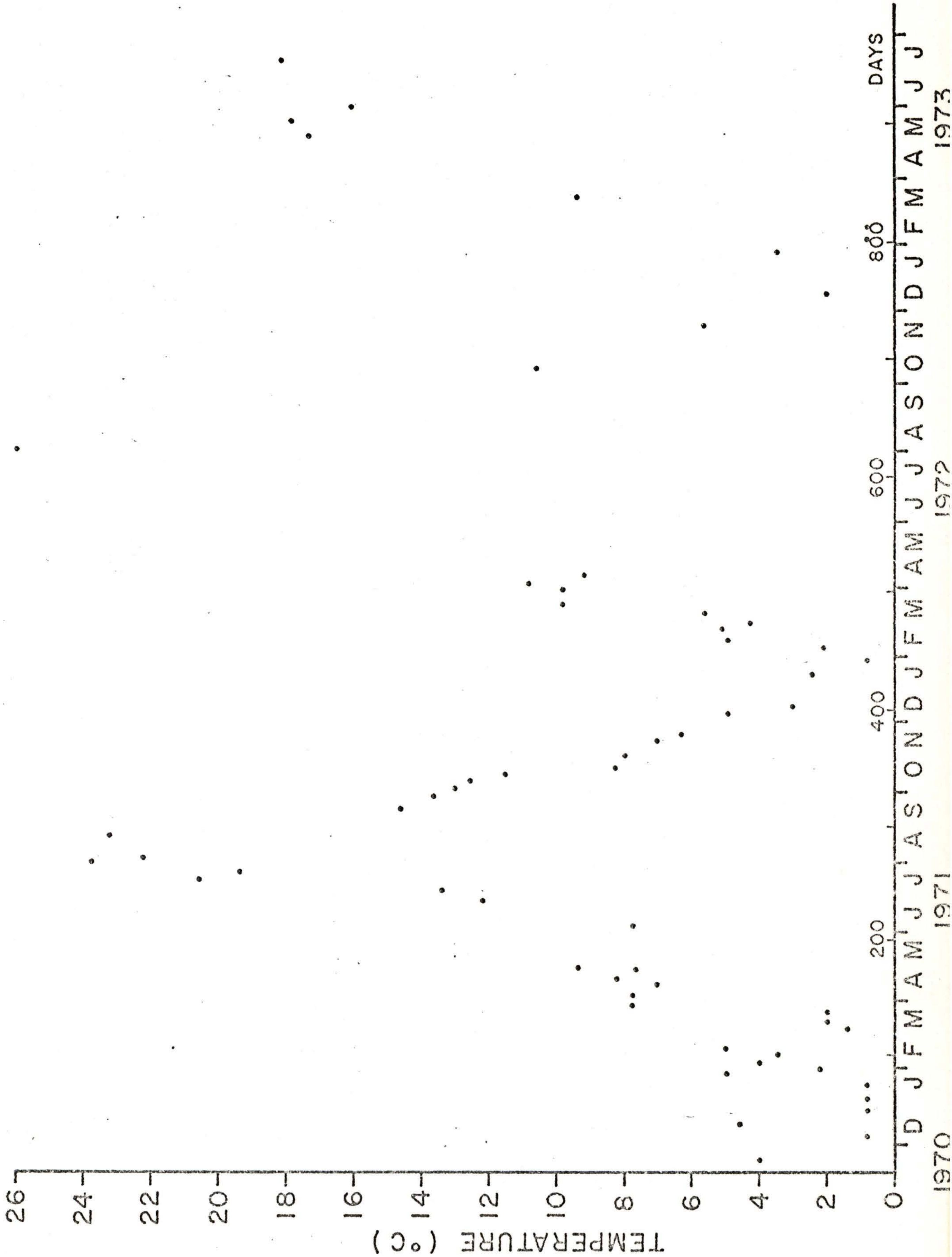
Date	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1941-1970 max	58	65	68	74	85	92	97	92	88	78	64	61
1941-1970 min	4	5	16	25	31	37	41	42	30	25	8	6
1941-1970 mean max	53.3	55.3	59.2	65.5	75.3	79.4	84.4	82.3	79.6	68	57.8	54.6
1941-1970 mean min	19.5	23.7	26.7	31.1	35.3	42.4	45.7	45.6	39.4	32.3	27.8	22.3
1971 max	56	57	57	76	79	75	88	87	72	67	54	49
1972 max	51	55	59	63	83	76	85	86	85	67	57	54
1971 min	20	25	25	31	35	41	41	46	38	25	27	17
1972 min	16	19	27	30	38	42	44	44	30	25	24	11

annual mean, 1941-1970 49.2

annual mean, 1971 48.5

annual mean, 1972, 47.9

AMBIENT TEMPERATURE, °F., BLINKHORN LAKE, 1941 - 1972 (Environment Canada, 1974).


TEMPERATURE (°C)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
DAYS
200
400
600
800
D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J
1970
1971
1972
1973

APPENDIX 6 - PRECIPITATION IN THE BLINKHORN LAKE AREA

Date	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
+ 1941-1970 mean	8.62	4.80	3.54	2.45	1.29	1.14	.82	1.04	1.85	4.91	6.78	8.88	46.12
1971	10.38	5.83	6.36	.60	.60	1.32	.13	.24	1.86	5.33	5.94	7.64	46.97
1972	12.8	9.67	9.33	.14	.14	.68	2.85	.66	3.4	1.49	2.62	11.81	57.98

+ Victoria Highland Records, within same precipitation Isopleth as Blinkhorn Lake (Roemer, 1972)

PRECIPITATION (INCHES) IN THE BLINKHORN LAKE AREA (Environment Canada, 1974).

APPENDIX 7

FIXING AND STAINING PROCEDURE FOR AMPHIBIAN GONAD

1. 10% formalin, 24 hours minimum
2. wash in water
3. transfer to 50% ethanol, 1 hour
4. transfer to 70% ethanol, 1 hour
5. transfer to 95% ethanol, 1½ hours
6. transfer to absolute ethanol #1, ½ hour
7. transfer to absolute ethanol #2, 1 hour
8. transfer to toluene #1, ½ hour
9. transfer to toluene #2, 1 hour
10. transfer to melted paraffin #1, 1½ hours
11. transfer to melted paraffin #2, 1½ hours
12. transfer to melted paraplast #1, 1½ hours
13. transfer to melted paraplast #2, 1 hour
14. embed
15. section and adhere to slide
16. toluene #1, 2-3 minutes or longer
17. toluene #2, 2-3 minutes or longer
18. absolute ethanol #1, 2-3 minutes or longer
19. absolute ethanol #2, 2-3 minutes or longer
20. 95% ethanol, 2-3 minutes or longer
21. 70% ethanol, 2-3 minutes or longer
22. distilled water, 2-3 minutes or longer
23. hematoxylin, Harris', 10 minutes
24. tap water, rinse
25. .5N HCl to destain, 3 minutes
26. running tap water rinse, 15 minutes
27. distilled rinse, few dips
28. 70% ethanol, 1 or 2 dips
29. eosin counterstain, 10 seconds
30. 95% ethanol to destain, 10 minutes
31. absolute ethanol, few dips
32. absolute ethanol, few dips
33. toluene #3, 2-3 minutes or longer
34. toluene #4, 2-3 minutes or longer
35. mount with histoclad - keep sections moist at all times

APPENDIX 8 - GLOSSARY[1]

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[1] taken partly from Rugh (1951) and Miller and Robbins (1954)

ampulla - see seminiferous tubule

cord - contains somatic cells and primordial germ cells, the primary spermatogonia. Connects the lobes of a multiple testis

epigonad - cord growing posteriorly from the cortex of the most posterior testis lobe. Contains primary spermatogonia and somatic cells.

glandular tissue - postbreeding tissue of seminiferous tubules within the mature lobule. Formed of Sertoli cells and connective tissue cytoplasm. This is totally resorbed shortly after its formation.

lobe - see testis

lobule, immature - anterior portion of the testis containing secondary spermatogonia and spermatocytes to be used for breeding in two years' time. Forms 20 - 25% of a breeding male's testicular mass. No cellular division occurs within this lobule until after the mature, postbreeding lobule's glandular tissue is formed. It then enlarges to fill the entire testis as the former is resorbed, and is eventually divided by the transition zone.

lobule, mature - posterior portion of testis containing mature or maturing tissue to be used for reproduction the next breeding season. Forms 75 - 80% of the breeding male's testicular mass. After reproduction this lobule is totally resorbed.

primary spermatocytes - stage in spermatogenesis derived meiotically from secondary spermatogonia and about half their size. Have a large, lightly - staining nucleus and clear cytoplasm.

primary spermatogonia - primordial diploid germ cells of male gonads, each with a lobed, vesiculated nucleus. Normally found within the cord. A supply of residual primary spermatogonia is always present within the cord.

progonad - cord growing anteriorly from the cortex of the most anterior testis lobe. Contains somatic cells and primary spermatogonia. New lobes form anterior to a constriction in the progonad.

secondary spermatocyte - stage in spermatogenesis derived mitotically from primary spermatocytes and about half their size. Has a darkly - staining nucleus and dark cytoplasm.

secondary spermatogonia - derived mitotically from the primary spermatogonia, a diploid stage with clear cytoplasm and a round nucleus. May divide mitotically several times before forming primary spermatocytes.

seminiferous tubules - basic testis divisions derived from rete cords, covered by a connective tissue theca and containing Sertoli cells and all stages of spermatogenesis. Normally sex cells in one tubule are in the same stage of spermatogenesis. Also called ampullae.

Sertoli cells - found within seminiferous tubules. Functionally similar to ovarian follicle cells since thay provide nutrients to maturing spermatozoa. Adult spermatozoa heads are embedded in Sertoli cell cytoplasm. Also called nurse cells. After sperm evacuation, Sertoli cells phagocytize intratubular debris.

sperm duct - see Wolffian duct

spermatid - haploid stage in spermatogenesis derived meiotically from secondary spermatocytes and about half their size. Darkly - staining with a nucleus of irregular shape. Metamorphose into spermatozoa.

testis - male gonad composed of seminiferous tubules. Matures anterior to posterior and is normally divided into two distinct parts, or lobules, separated by a transition zone. Normally contains all stages of spermatogenesis except the primary spermatogonia. *T. granulosa* has a multiple testis; young males have two lobes, older males form additional lobes up to a maximum of six, three per side.

transition zone - composed of connective tissue that separates the maturing from the immature testis lobule. The post-breeding immature lobule ceases all mitotic activity once this zone is formed.

Wolffian duct - sperm or mesonephric duct connecting with testis via efferent ducts. Transports sperm outside the body.

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Title of Thesis

Habitat Selection and its Relation to Reproductive Development of the Rough-Skinned Newt, *Taricha granulosa* on Southern Vancouver Island.

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MAY 3, 1974
Date