THE ECOLOGY OF COEXISTENCE IN TWO CLOSELY RELATED SPECIES OF FROGS (RANA)

by

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ABSTRACT

The red-legged frog, Rana aurora aurora and the western spotted frog, Rana pretiosa pretiosa, were found co-existing in southwestern British Columbia. The locality – the upper Little Campbell River near White Rock – is the only area in the Pacific Northwest in which the two species are known to be sympatric. Little was known about the biology of the frogs, which are closely related and resemble each other in habits; finding a sympatric locality provided a unique opportunity to study how they manage to coexist and avoid competitive exclusion. The study involved finding the ecological requirements during the nonbreeding season and finding the reproductive isolating mechanisms.

The study revealed that R. pretiosa is much more aquatic than R. aurora. The affinity of R. aurora for land and R. pretiosa for water is the basic ecological difference permitting them to coexist.

The morphology, ecology, and behavior of the frogs are adapted to their preference for land or water. R. aurora has relatively longer hind limbs than R. pretiosa; but the feet of R. pretiosa are more extensively webbed. The eyes of R. aurora face laterally; those of R. pretiosa face upwards. The skin of R. pretiosa is covered with a thick mucous coating; that of R. aurora is smooth.

There is much overlap in the diet of these species; they share as much as 88% of the kinds of foods most commonly eaten, and 75% of the food items most abundantly eaten. At

times they feed within close proximity of each other; however, R. aurora feeds predominantly on land, whereas R. pretiosa feeds predominantly from water.

Body temperatures of wild frogs in the field were significantly different. R. pretiosa attains higher body temperatures than R. aurora, indicating divergent preferences in habitat requirements. R. pretiosa has a higher temperature tolerance than R. aurora. R. pretiosa uses water to thermoregulate, while R. aurora uses shade and sun on land.

The rate of evaporative water loss and water loss leading to lethal desiccation were the same in both species, indicating no obvious physiological basis for their water or land preferences.

To escape from predators, R. aurora uses land and R. pretiosa uses water. R. aurora is a strong jumper, and jumps in a nearly straight path at an angle of 45°; R. pretiosa is a weaker jumper and jumps in a circle at an angle of about 10° to the ground, but normally escapes by submerging to the bottom of the nearest water.

Both species breed during the same two to four weeks in February and March within a few feet of one another in the same bodies of water. They avoid interbreeding, however, by means of such premating isolating mechanisms as differences in mating call, male calling behavior, and microgeographic choice of spawning sites.

Embryos of each species have different thermal adaptations and requirements which are correlated with adult breeding

habits. For example, R. pretiosa females deposit eggs in very shallow water exposing them to relatively high daytime temperatures. R. aurora deposits eggs beneath several feet of water buffering them from heat stress and wide thermal fluctuations.

Factors underlying their rare occurrence in sympatry and observed geographic distributions are discussed in terms of their habitat requirements and the present existence of other species of ranid frogs in the Pacific Northwest.

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I thank Dr. J.D. McPhail for his considerate supervision throughout this study. He, Dr. D.H. Chitty, Dr. N.R. Liley, and Dr. G.G. Scudder beneficially criticized rough drafts of this thesis. Douglas Hay accompanied me on many trips to the field; I appreciate his assistance and friendship. I thank Vinnie McQueen for taking special care in typing the thesis. The Fraser Valley Parks Board allowed me to use park land as a study area.

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INTRODUCTION

In northwestern North America, there are seven species of frogs belonging to the genus <u>Rana</u>. Within this <u>Rana</u> species group are two closely related species: the red-legged frog, <u>Rana aurora aurora</u> Baird and Girard, and the western spotted frog, <u>Rana pretiosa pretiosa</u> Baird and Girard. The distribution of <u>R</u>. <u>aurora</u> is in coastal areas from southwestern British Columbia, southwards through Washington, Oregon, and California. The distribution of <u>R</u>. <u>pretiosa</u> is more extensive, and this species ranges from southeastern Alaska, south through British Columbia, Washington, and Oregon, to northern Nevada and Utah, and eastward through Saskatchewan, Idaho, western Montana, and Wyoming (Stebbins 1951). The distributions of the two species are seen in Fig. 1. One striking feature of the distributions of the two frogs is that, except for a few isolated localities in western Washington and Oregon, their ranges are entirely complementary (the ranges do not overlap). Moreover, the present existence of <u>R</u>. <u>pretiosa</u> in western Washington localities, where the species are said to be sympatric, is doubtful (Dumas 1966).

In British Columbia, <u>R</u>. <u>pretiosa</u> is reported to occur only east of the Coast Range mountains, while <u>R</u>. <u>aurora</u> is restricted to the coastal areas west of these mountains (Carl and Cowan 1945). (Two specimens of <u>R</u>. <u>pretiosa</u> were collected in 1941 on Nicomen Island, an area which is west of the Coast mountains (Carl and Cowan 1945), but this population has not been rediscovered). However, in 1967 I discovered a locality in southwestern B.C. where <u>R</u>. <u>aurora</u> and <u>R</u>. <u>pretiosa</u> occur

Figure 1

Geographic distribution of <u>Rana</u> <u>aurora</u> and <u>Rana</u> <u>pretiosa</u>.
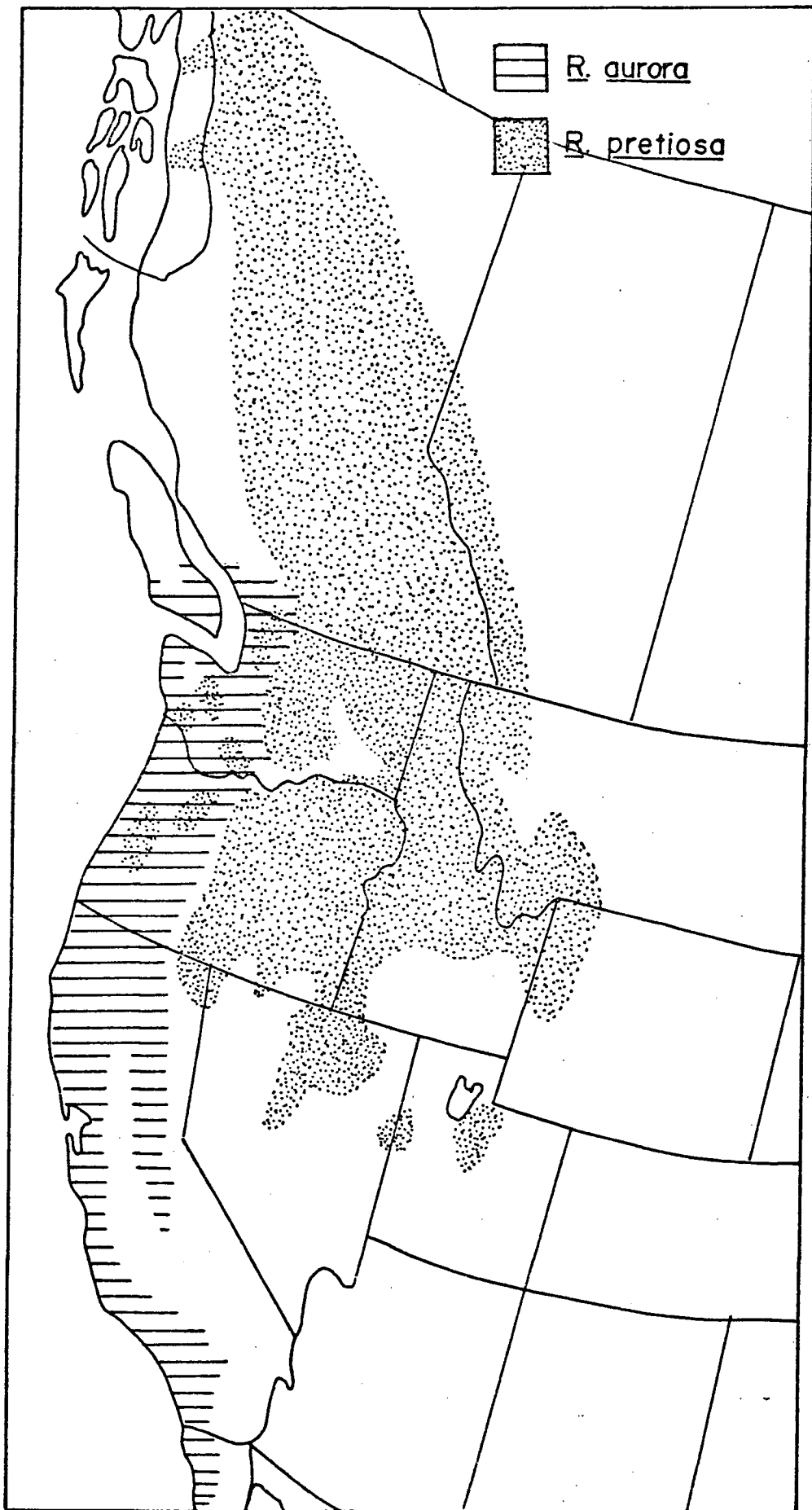
R. aurora
R. pretiosa

sympatrically. This locality, the upper Little Campbell River, represents the only known area where the species coexist.

Little is known about the biology of either species. Storm (1960) studied aspects of the breeding biology of R. aurora in Oregon, and Turner (1958, 1960) studied R. pretiosa at 7800 ft in Wyoming. Almost nothing is known about the biology of these species in British Columbia (Carl 1966). Stebbins (1954), however, indicates that both species are very closely related and resemble each other in habits; naturalists often confused the two species.

If related species' ecological requirements are sufficiently similar, the existence of one species may control the presence or absence of another. Competitive exclusion may result if related species' requirements greatly overlap (Gause 1934). The discovery of these closely related species in sympatry provides a nearly unique opportunity to study how they achieve successful coexistence and avoid competitive exclusion. Many other studies have been carried out on niche diversity and coexistence in other vertebrate groups, especially mammals and birds (Lack 1945, MacArthur 1958), but anuran vertebrates have not been closely investigated in this regard.

The ability of related species to coexist must be attained in both breeding and nonbreeding activities, and the question of how R. aurora and R. pretiosa succeed has been divided into two components: what are their ecological require-ments and how do these permit coexistence, and how does each species remain as an independent breeding population, i.e., what are the reproductive isolating mechanisms that prevent

interbreeding between the species?

Observations and experiments throughout the study revealed that R. pretiosa is more aquatic than R. aurora. The affinity of R. aurora for land and R. pretiosa for water is a basic ecological difference, and the water-land boundary is crucial. This difference underlies most aspects of their comparative ecology and behavior, and provides the basis for understanding the mechanisms by which they coexist. The morphology, ecology, and behavior of the frogs are adapted to their preference or restriction to water or land. How these adaptations allow coexistence of the two species is the topic studied in this thesis.

STUDY AREA

Both species, R. aurora and R. pretiosa, occur in marshes about 5 miles east of White Rock, B.C. A 7-acre field, about 220 ft above sea level, and near the junction of North Bluff and Carvolth Roads in Langley Electoral District, was used as the site of field studies. Research began in October 1967 and ended in July 1970.

The area is wet flat lowland, covered predominantly by bulrushes (Juncus effusus), sedges (Carex sp.), and buttercups (Ranunculus repens). Ranunculus forms almost a complete carpet throughout the field. The other two plant types are abundant but scattered throughout the whole area. The eastern and western borders of the field are alder, birch, and coniferous woods, the southern border is more lowland marsh, and the northern side is interrupted by an asphalt road, across which is more lowland. The woods along the eastern edge of the study area lie on a hill with an incline of about 40°. This steep hill terminates above the field in pasture.

A permanent slow-moving stream, the Little Campbell River, flows through the centre of the field. The study site is referred to as the LCR study area. The river margins fluctuate considerably during the spring rains, from February through April, and the width may vary from 5 to 100 ft in a few days. In wet periods during the spring, the shallow overflow is usually not more than 1-3 ft deep, and after several days without rain this overflow subsides, leaving the main channel about 5-15 ft wide. The channel depth varies from 2-6 ft in the center, to 6-18 inches on the gradually sloping edges. There is little

current in the river except after heavy spring rains.

The river bottom is soft mud covered by rotting vegetation. During the summer the river is low and is filled with a dense growth of Nuphar, Lemna, Potamogeton, and Myriophyllum. Carex, Juncus, Typha, and Ranunculus grow profusely along the banks, but the continually fluctuating river level usually leaves a strip of exposed mud along the river course.

A temporary pond, about 40 by 200 ft, and 6-36 inches deep, lies 90 ft west of the river where it flows beneath a bridge. The south half of the pond is dry by May or June, but the northern half remains filled until July, and then refills again in September. The pond is thick with water purslane (Ludwigia), and Potamogeton. The bottom is covered with dead macrophytes, and a thick cover of Juncus surrounds the pond perimeter.

A map of the study area is seen in Fig. 2, and views of the river, field, and pond are seen in Figs. 3-6.

After a day or more of rain during the spring, numerous rainpools dot the field. These pools vary in area, from small puddles to larger pools about 2-3 ft square. At times, channels form from the large pools to the river. The pools are usually 2-4 inches deep with a soft mud bottom. They tend to reform in the same places within the field, where the ground is depressed and low. They remain filled for several weeks during the spring, but by June, with warm weather and less rain, they dry. With heavy summer rains they may refill, but dry again after a few days. By September, the pools are again filled with the onset

of autumn rains, and they persist throughout the winter.

Other amphibians live in the field in addition to
R. aurora and R. pretiosa. They include the anurans, Hyla
regilla and Bufo boreas, and the urodeles, Ambystoma gracile,
Ambystoma macrodactylum, and Taricha granulosa. In June 1970,
the first bullfrogs, Rana catesbeiana, were seen and caught in
the LCR study area.

During the summers of 1968 and 1969, the field was used
sporadically as pasture for 30-40 head of cattle. They cropped
the vegetation, mainly the Ranunculus. The study area was closed
to the public, and consequently, there was minimal disturbance
by humans to the frogs or their habitat.

Figure 2

Map of study area where _Rana aurora_ and _Rana pretiosa_ are sympatric.

0

50'

N

River

River
Overflow

Woods

Woods

Pond

Road
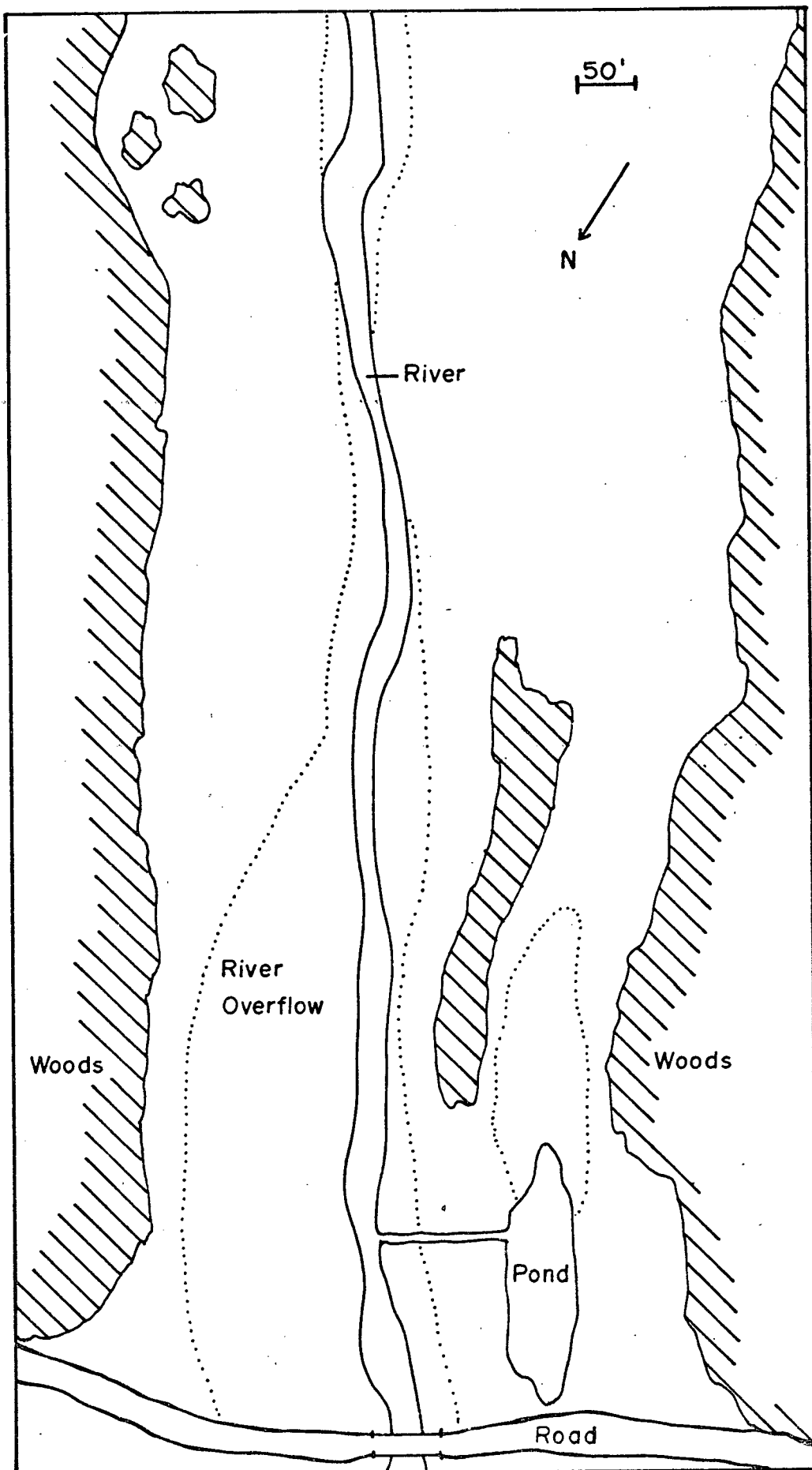
Figure 3

Little Campbell River at time of spring overflow. View looking

south in study area.

Figure 4

Main channel of Little Campbell River. View looking south in study area.

Figure 5

Little Campbell River in foreground and breeding pool in background. View looking west in study area.

Figure 6

Breeding pond nearly dry in June.

MATERIALS AND METHODS

I used a combination of field and laboratory observations and experiments to compare the ecology and behavior of the frogs.

A. Morphology

As part of a concurrent study on the population dynamics and growth of the two species of frogs, I measured the body size and limb length of several hundred frogs caught in the field. Information on maximum body size, age and size at sexual maturity, and several morphological characteristics were gathered at this time.

The body size (snout-vent length) of each frog was measured by holding a frog by its hind limbs, stretched out venter down on my knee. A measurement was made by placing a clear plastic ruler on the back of the frog and taking the reading (to the nearest millimeter) from the tip of the snout to the cloacal opening. The size of the right hind limb of a frog was measured by holding a plastic ruler alongside the limb and the measurement was taken from the middle of the cloacal aperature to the tip of the outstretched 4th digit on the hind foot. Usually two or three measurements were made of both body and leg size to reduce error in measurements.

B. Ecology

a. Habitat Preference

During visits to the study area, I took special notice of where frogs were captured. The type of substrate on which the frog was found - land or water - was recorded for most captures throughout the study.

Laboratory tests on habitat preference were conducted. Frogs used had been raised from eggs in the laboratory and after metamorphosis were kept in glass stacking dishes. The frogs had metamorphosed from the tadpole stage one week before being used in tests.

A plastic swimming pool was used for these tests. The pool (8' x 4' x 1') was half filled with dirt (6 inches deep). A moat 3 ft long and 6 inches deep was dug out in the center of the pool and filled with water and water purslane (Ludwigia). This testing arena is pictured in Fig. 7. It was placed on the floor of the laboratory, and a plywood partition built around it to screen the observer from the animals. Temperature of the room during this study was 20 C.

Frogs were placed in this pool in the same spot on each test (see x in Fig. 7). During the following 30 min the positions of the frogs were recorded twice - each 15 min interval. A frog was recorded as being either in land or water. (After precisely 30 min a snake was introduced into the arena for studies on predation to be described later).

b. Food and Feeding Behavior

In 1968, from May to October, frogs were collected from adjacent marshes for analysis of their stomach contents. Frogs were collected in habitats like those in the LCR study area, so that conclusions about feeding could be applied to the undisturbed study area populations. Within each month, frogs of both species were caught on the same days. They were usually taken in the same vicinity, only a few feet apart, so that the food in their intestinal tracts represented prey items that

Figure 7

Top view of plastic swimming pool used as testing arena for predation tests with snakes.

mud

water & water purslane

8'

6'

1'

4'

X
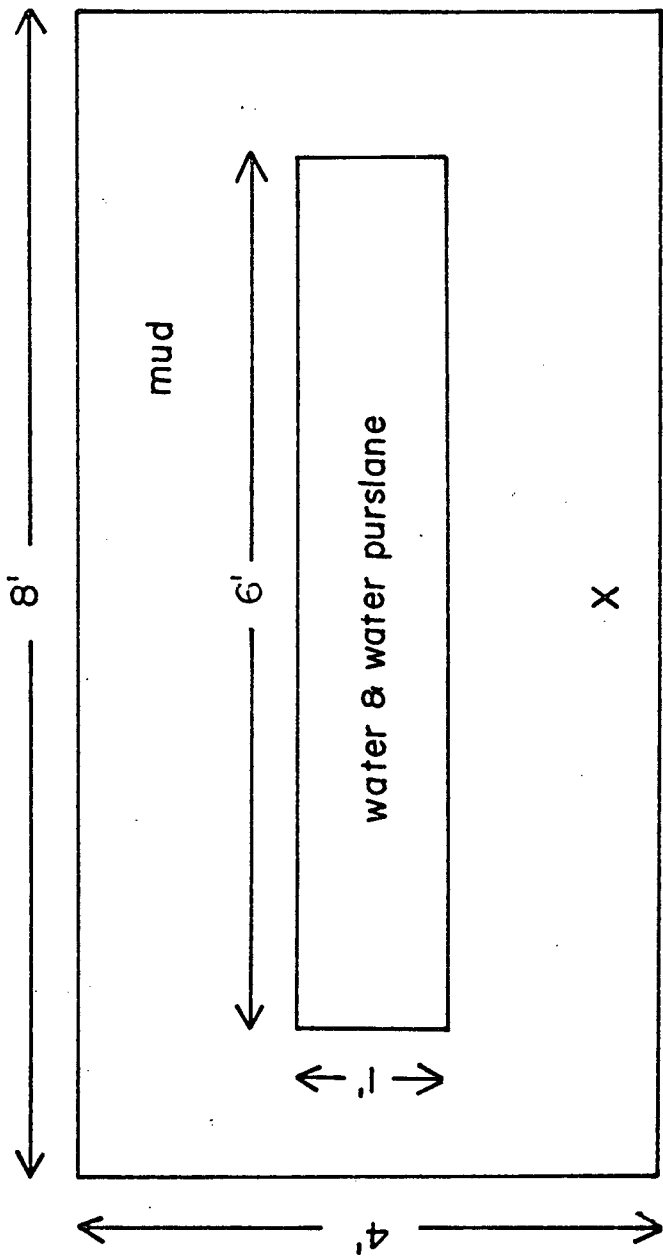
were probably available to both species.

I walked along the river margins and through the vegetation and attempted to catch all frogs seen on those days set aside for the purpose of food analysis. After capture, each frog was killed and preserved in a 5% formalin solution. At a later date, the entire intestinal tract was removed from each specimen, and all animal remains were identified. All insect remains were identified when possible, to family level (with the exception of Plecoptera and Trichoptera), and to growth stage (adults or larvae). All spiders were listed as arachnids and not classified further. Only two kinds of molluscs were eaten: slugs and snails. They are listed as such.

I did the analysis of food to obtain two kinds of data: the total number of food items of each kind found in all stomachs, and the number of stomachs containing a particular kind of food items. These data were compiled for R. aurora and R. pretiosa separately. Moreover, each species was divided into two group- ings: newly metamorphosed frogs of the season, and frogs 1 year old and older. Each grouping was treated separately.

The primary aim of stomach analysis was to determine the degree of overlap in food items taken by the species. The amount of overlap in diets might provide an indication of competition for certain food items. Similarity in diets was determined by comparing the kinds and numbers of prey eaten by each species, and the subgroup within each species. All food items were tabulated, and the ratio of the number of food items shared between the two species, over the total number of food items for each species, yielded the percentage overlap in diet.

For example, R. aurora (both subgroups) exploited 53 food items; R. pretiosa exploited 49 food items. Thirty of these food items were common to both species. Therefore, R. aurora shares 30/53 or 56.6% of the food items it exploits with R. pretiosa, and R. pretiosa shares 30/49 or 61.2% of its food items with R. aurora. This method of determining percentage overlap in diet is used to compare sympatric bird species and was justified by Holmes and Pitelka (1968).

The dominant food items in the diet of each species are listed. These were calculated in two ways: the eight most abundant items in all stomachs within each species group; and the eight food items that appeared most frequently in the frogs' stomachs regardless of their abundance in the stomachs. For both newly metamorphosed individuals and frogs 1 year and older of each species, the top eight items make up over 50% of all food eaten. The remaining items were represented only infrequently.

1) Natural feeding behavior observations

Occasionally during the study, I used binoculars or my unaided eye to observe the natural feeding behavior of frogs that were unaware or at least, not obviously frightened by my presence. I watched their movements and orientation response to potential nearby prey. Of special importance was the type of substrate that feeding activities occurred on and the general hunting patterns of the frogs. At times I threw certain food items to frogs and watched their behavior. These casual and detailed feeding observations of feeding behavior only allow qualitative description of their feeding activities.

2) <u>Laboratory feeding tests</u>

In the laboratory, an attempt was made to determine the feeding efficiencies of both species under different habitat conditions.

A supply of laboratory-raised frogs was kept for use in behavioral experiments. These animals were raised from eggs in the laboratory and maintained under known conditions. Thus, for the behavioral studies, most of the compared traits probably had a genetic rather than environmental basis.

Frogs used in feeding tests were laboratory-reared and were tested just shortly after metamorphosis. All of the frogs used were 25-29 mm sv length, and weighed 1-1.8 g. The frogs were tested under wet and dry conditions. Three glass stacking dishes (18 cm in diameter) were filled with 1 cm of water. Three other dishes were left dry. Two <u>R</u>. <u>aurora</u> and two <u>R</u>. <u>pretiosa</u> were placed in each dish. On a testing day, 20-30 fruit flies (<u>Drosophila</u>) were introduced into the dish. For the following 10 min, the number of times each frog made a snap at a fly and the number of snaps that were successful (a fly captured) were recorded. This procedure was repeated every two days, for both wet and dry bowls, until five trials were completed for each bowl. The frogs were not fed between trials as an attempt to maintain their hunger at the same level for each testing day.

These tests yielded some information on the feeding capabilities of frogs in wet and dry conditions, but unfortunately, the effect of intraspecific and interspecific competition among the four individuals in each dish is a confusing factor. Chi square tests were used to test the significance of results.

The results for all wet tests and all dry tests were pooled and treated separately. Actually the analysis of variance is the correct statistical test for this experiment, but because the tests were not rigidly controlled, Chi square tests on pooled data are sufficient to yield meaningful probabilities.

3) Starvation tests

The ability of small frogs to survive without food was investigated. Newly transformed laboratory-reared frogs were kept in glass stacking dishes with a layer of moist sterile dirt on the bottom. Temperatures with the bowls were 17-20 C. Ten frogs of each species, 5 per bowl, were maintained without food until 5 of each species had died. The number of days until each death was recorded. After half of each species had died, the survivors at that time were given fruit flies in abundance. Further mortality and survival were recorded.

c. Environmental Physiology - Temperature

1) Field and frog temperatures

The effect of temperature on the comparative ecology of the frogs was examined in several ways.

Upon arrival at the LCR study area, I recorded the air and water temperatures. On many days I recorded the cloacal temperature, that is, the internal body temperature, of every frog I caught. This was done immediately upon capture with a rapid reading Schulteis cloacal thermometer. After the frog's temperature was taken, I recorded the air or water temperature in the place where the frog was caught. The air temperature (dry bulb) was that at the level of the frog's body, a few cm

off the ground. Water temperatures were measured at the water surface. Cloacal temperatures were measured on days of varying climatic conditions (from bright sun to heavy rain) in an attempt to establish the upper and lower thermal regimes of wild frogs.

2) Frog temperature tolerance

A common method of establishing anuran temperature tolerances is to find the 'critical thermal maxima' (CTM). This is defined as "the thermal point at which locomotory activity becomes disorganized and the animal loses its ability to escape from conditions that will promptly lead to its death" (Cowles and Bogart 1944). Hutchison (1961) provided a standard methodology for tests of CTM. Basically it involves slowly raising the temperature until the animal shows stress symptoms. The temperature at which the animal shows stress symptoms is the critical thermal maximum. In this study I followed a slightly different procedure, but one that appears more ecologically relevant. Instead of continually raising the temperature until a frog showed stress symptoms I raised the temperature to a fixed limit and allowed the animal to remain at that temperature for three hours. If a frog survived for at least three hours at a given high temperature (without showing signs of stress), it is likely that temperatures below that level are within the range allowing normal activities. Subjecting assay animals for a length of time to one temperature gives a better indication of how that animal responds, than does watching its behavior with a brief exposure to a very high and changing temperature level. In standard CTM tests, temperatures below the CTM may not be lethal, but may cause stress symptoms that only develop

after a long exposure of time, that is, after the temperature has already been increased to another higher point. Thus the limited time allowed at temperatures slightly below the CTM may be more harmful than CTM tests show, because there was insufficient time for the symptoms to become manifest.

Frogs were tested in the following manner. A 10-gallon aquarium was divided into two with a wire mesh. A Bronwill water circulator in one half heated the water of the entire aquarium. The aquarium was filled to capacity and wire mesh placed on top. Frogs to be tested were placed in one side of the tank. They were covered entirely by water, but could extend their nostrils out at the top. Frogs were introduced into the aquarium at 18 C, and the temperature was raised to the preset limit in 15-30 min. The desired temperature was maintained for three hours and the behavior of the frogs recorded. Death was defined as that point when frogs sank to the bottom of the tank and no longer responded to a pinch by tweezers; the time till death was recorded.

Frogs used were both laboratory-reared and wild-caught. All frogs were maintained from 18-20 C for about 5 days prior to testing. Frogs were tested in temperatures from 27-35 C.

d. Water Balance

1) Dehydration

A vital problem confronting anurans is that of proper water balance and the avoidance of desiccation; paramount to their survival is the maintenance of a moist skin.

The difference in habitat preference of the two frogs

may result from divergent problems in water balance, and a comparison of the rates of evaporative water loss was made with both species. Frogs of all sizes (laboratory-reared and wild-caught) were used. All frogs tested were maintained for one week at 18 C before testing; they were held in tanks and provided with water and no food.

Wire mesh boxes, either 4 or 6 inches square, were made to hold the frogs. A cage with a single frog enclosed was suspended by a string so that all sides of the cage were exposed to air. Before being enclosed, the frog was forced to release all bladder water by having a small rubber tube put into its cloaca and pressure being applied to the bladder.

At the beginning of each test, frogs were weighed to the nearest .05 g. The cage and frog were weighed together to avoid directly handling the frog. Every hour thereafter, the frog was again weighed. Frogs were exposed to still air at two different temperatures and humidities: 15 C and 60% humidity, and 28 C and 25% humidity.

At 15 C, the tests with the large frogs were terminated after 6 hours, but small frogs were desiccated until the lethal limit was reached. These frogs were considered dead when they could no longer right themselves if turned onto their backs. This endpoint is a standard one for tests of desiccation limits with anurans (Heatwole et al 1969). When the lethal limit was reached, the frog was reweighed, and the percentage of body weight lost was determined. The survival time was recorded.

At 28 C, all frogs were desiccated until death occurred. Again the time till death and percentage weight lost were

determined.

For all frogs tested at 15 and 28 C, the rate of
evaporative water loss per hour was calculated and the hourly
average determined.

Healthy frogs of each species that were not used in
desiccation tests were sacrificed and placed in an oven of
110 C for 48 hours. The percentage of their initial body weight
comprised of water was ascertained by comparing their wet and
dry weights.

2) Submergence tests

The ability of frogs to withstand submergence under
water was investigated. Ten frogs of each species, all 28-33 mm
sv length, and 1.5 - 3.2 g, were kept submerged in a tank through
which water 10 C was flowing. Frogs were kept submerged for
eight hours and their behavior and survival recorded.

e. Predators and Predator Avoidance

1) Field tests

Throughout the study, as I searched for frogs in the
field, I took special notice of their escape responses. On some
days, when I was assisted in my searches for frogs, I performed
tests to gain insight into the frogs' escape responses. After
a frog was caught and then ready for release, I placed it
parallel to the river bank, 1-2 ft from water, between me and
my companion. I then scored its escape behavior as being either
directly to land or to the water. If it went into the water, it
was scored as either immediately submerging or remaining on the
water surface.

2) Laboratory escape behavior

One of the major predators of frogs in the LCR study area is the garter snake, Thamnophis sirtalis. Snakes collected from the study area were used as predators in laboratory studies of frog escape behavior. Naive laboratory-reared frogs were used as the prey. Since these frogs had never encountered natural predators of any kind, learning was not an important aspect of their initial escape responses.

Predation tests with snakes and frogs were conducted in the plastic swimming pool previously described and pictured in Fig. 7. Either one or two frogs of each species (all 26-32 mm sv length) were placed midway along one side of the pool (see x in Fig. 7). They were undisturbed for 30 minutes. After the 30 minutes had passed, I placed a garter snake in the pool at the same place where the frogs were introduced, regardless of the position of the frogs in the pool. The position of the frogs and notes of their movements relative to the movements of the snake were recorded. Trials were continued for a maximum of 2 hours, or until a frog was caught by a snake.

The snakes used were caught in marshes adjacent to the LCR study area and had probably had experience with both R. aurora and R. pretiosa as prey. The snakes were kept for 10 days in the laboratory with only water and no food so as to increase their hunger level and hunting behavior before being used as predators.

The confines of the pool probably affected the snakes' chances of catching frogs. However, the aim of these tests was to study the frogs' behavior and pattern of escape rather than

the number eaten and time till capture. Each test was run with naive frogs so that specific differences in escape patterns between R. aurora and R. pretiosa were apparent.

3) Frog jumping ability

Laboratory-reared and wild-caught frogs were used for making comparisons of jumping abilities. Frogs of varying body lengths were used and the sv length and hind limb length were measured on all individuals. An individual frog was placed on the mud of the plastic swimming pool (Fig. 7), (the moat in the center was filled in), and allowed to jump spontaneously. The distance between jumps was measured to the nearest cm. Over a period of six days, each frog had 30-45 jumps measured, and the longest 10 jumps for each animal were selected for comparison.

4) Predators

Known vertebrate and invertebrate predators of anurans which occurred in the LCR study area were recorded throughout the study.

C. Comparative Reproductive Behavior

How the frogs are reproductively isolated is an important aspect of how they successfully coexist during breeding activities. Information has accumulated on both species during the breeding seasons of 1968 and 1969. Material, unless otherwise specified, is based on data from the LCR study area, where both species are sympatric. However, two other areas, where only R. aurora is found, were also observed, as a means of determining if this species differed because of sympatry with

<u>R</u>. <u>pretiosa</u>.

One locality is a small pond at sea level adjacent to Beaver Lake in Stanley Park, Vancouver, B.C. The pond, formed by overflow from a large lake, is about 15 by 40 ft, and 6-18 inches deep. The water is clear and allows good visibility of the frogs that breed in it. Most breeding occurs in the deeper muddy lake nearby.

The second area is Marion Lake in the University of British Columbia Forestry Reserve, about 1000 ft in elevation near Haney, B.C. The lake is 32 acres in area, with a mean depth of 8 ft. The water is very clear and allows good vision of the several hundred <u>R</u>. <u>aurora</u> that breed in it. A thick coniferous forest extends to the lake on all sides.

In both years, continuously recording thermographs (Ryan Model D) were submerged in the center of the LCR study area pond, at a depth of 2 ft. In 1969, continuous air temperatures were taken near the pond. In 1969, recorders did not measure below 0 C. The thermograph in air was not exposed to direct sunlight and thus provided the maximum temperatures in the shade throughout the day. For 1968, air temperatures are from the Vancouver airport, about 20 miles to the north of the LCR study area, and the data are corrected for known differences between the two localities. Precipitation records for both years are from the airport station.

Frog vocalizations were recorded with a Uher M514 microphone, and an LC-10 hydrophone (Atlantic Research Co.), and a Uher 4000 Report-L tape recorder. Calls were analyzed on a Sonagraph (Kay Electric), adequate tests being made to ensure

that calls were not distorted if recorded with different
equipment.

The intensity of the calls as they occur in the natural
environment, were measured with a Scott Type 450 sound level
meter.

D. Embryonic Thermal Requirements and Environmental Temperatures

In addition to the breeding behavior of the sympatric
frogs, what is important to know is how each species faces
similar selective pressures with regard to other aspects of
their breeding biology. One major component of the environment,
impinging on almost all aspects of an anuran's life history, is
temperature.

The frog embryo is especially susceptible to thermal
stress since it is left to develop in the place where eggs were
deposited, and is unable to escape from adverse conditions. In
large part, the survival of embryos will depend on their thermal
requirements and adaptations. Moreover, Moore (1949) has pointed
out that embryonic thermal requirements are a major factor in
governing the geographic distributions of frogs.

Determination of the thermal requirements of embryos
of both species may provide further evidence on the mechanisms
by which R. aurora and R. pretiosa have achieved reproductive
success in sympatry.

a. Effects of Temperature on Egg Development

The basic experimental design for studying the eggs
was to maintain eggs at constant temperatures, examine them

periodically with a dissecting microscope, and note their progress in development. Efforts were made to examine the eggs at approximately 6-hour intervals, but more frequent examinations provided more precise data on the time between successive stages and endpoints for eggs tested near lethal thermal limits. Criteria for all stages were based on the staging system for Rana sylvatica (Pollister and Moore 1937).

Since the temperature tolerance of embryos increases with age (Brown 1967), a better analysis of lethal limits is obtained if eggs in very early stages are used in tolerance tests; the most restrictive thermal limits are those of young embryos. All spawn used were only a few hours old; the R. aurora eggs were in stage 4 (4-cell) and the R. pretiosa eggs were in stage 3 (2-cell) when most tolerance experiments were initiated.

The temperatures at which the young eggs of each species were maintained and examined for development varied within 2 C or less, except in the 15 C for R. aurora. Here the temperature varied almost 4 C. The high temperatures (> 20 C) were established in 10-gallon aquaria with use of Bronwill water circulators. The eggs were placed in well perforated plastic containers and submerged in constantly circulated and aerated water. The 15 C test for R. aurora was done in an aquarium held at room temperature. A Porta-Temp regulator kept the water of a 50-gallon tank at 10.8 C, and another tank was held at 7 C by adjusting the flow rate of declorinated water. For the lowest temperatures, eggs were kept in glass stacking dishes in a cold room at 4.5 C, and dishes containing other eggs were

kept on ice in the cold room. This provided temperatures of
1-3 C. At least 50 eggs of each species were tested at each
temperature.

The effect of temperature on the rate of development
was determined by examining 15-20 eggs in each group, and calcu-
lating the time between successive stages. When these eggs were
found to have progressed in stage, the number of hours between
observation periods was taken to be the actual interval between
the observed stages. In some instances it was apparent that
the eggs had been in the new stage for several hours, and thus
there are slight errors in estimating time between some stages.
More frequent examination of eggs at high temperatures reduced
these errors. However, the estimate of primary concern is the
total number of hours for the embryos to reach a designated
endpoint (described below). A comparison, relatively free of
error, of the effect of temperature on the rate of development
is obtained when the total number of hours for the embryos to
reach the standard endpoint is calculated.

Stage 20 (gill circulation) was chosen to indicate
completion of development. Since embryos of different species of
Rana hatch, (i.e., emerge from the jelly coats) at different
stages, for example, 19, 20, or 21, the time to hatching may not
be as good an endpoint for comparative purposes as a specific
stage in development. Consequently, when embryos reached stage
20 without obvious developmental abnormalities, they were
considered completely developed. Embryos that reached this
stage in apparently normal condition subsequently survived.
The actual stage for hatching (emergence from jelly), was

ascertained for both species.

The lethal temperatures for both species were defined as those at which either less than 50% of all the embryos in each group failed to reach stage 20, or they did so with obvious developmental abnormalities that resulted in subsequent mortality.

Some data on changes in temperature tolerance of embryos beyond stages 3 or 4 were obtained for both species. R. aurora eggs in stage 9 (late blastula) were held at 20, 21.5, 26, and 28 C (all $\pm$ .1 C) for the duration of their development. Another group of R. aurora eggs in stage 11 (gastrula) was maintained at 23 $\pm$ .1 C.

A set of R. pretiosa eggs in stage 5 (8-cell) was held at 30 $\pm$ .1 C and examined for developmental success. These eggs as well as all others used, were collected in the field.

b. Effects of Acute Cold Exposure on Survival

A series of tests was performed to determine if the embryos of both species were able to withstand short-term exposure to cold temperatures that were normally lethal to embryos in chronic exposure.

Embryos of both species were collected in the field and maintained for short periods in water of 1 and 3.5 C (both $\pm$ .5 C). Groups of R. pretiosa embryos in early stage 5 (8-cell) were kept in either 1 or 3.5 C for 4 hours. Different groups of R. pretiosa embryos in stage 7 (32-cell and morula) were placed in either 1 or 3.5 C for 2.5, 4, or 8 hours. Embryos of R. aurora in stage 9 (late blastula) were placed in 1 C

water for 2.5, 4, or 8 hours.

After exposure to low temperatures for the varying time intervals, each group of embryos (at least 50 for each group) was returned to room temperature (16-18 C) and allowed to continue development. The effect of the short-term cold exposure was determined by comparing the survival of test eggs with those of the controls (embryos from the same egg mass as test eggs but not subjected to cold shock). Control eggs were kept at room temperature at all times.

The low temperatures were similar to those occurring at night where the species breed, and the time intervals chosen approximated durations of cold exposure in the field.

c. Embryonic Oxygen Consumption

Embryos of both species in the same developmental stages were used for measuring O_2 consumption. Thirty embryos in early stage 12 (disappearing yolk plug) were placed in a 250 ml Erlenmeyer flask kept at 18.5 $\pm$ .1 C. There were 6 replicates (6 flasks each with 30 embryos) for each species. Some jelly was left attached to the eggs. The flasks were initially filled with air-saturated water and then sealed. After a period of 15 hours for R. aurora, and 18 hours for R. pretiosa, the O_2 consumption of the embryos within the flask was determined by analyzing a sample of water from each flask with use of a PO_2 Radiometer. Measurement of embryonic respiration is based on embryos progressing from stage 12 to early stage 15.

RESULTS

A. <u>Morphology</u>

In Amphibians of Western North America, Stebbins
(1951, 331-332) provides a key and contrasting descriptions of
<u>R</u>. <u>aurora</u> and <u>R</u>. <u>pretiosa</u>. Stebbins' descriptions are sufficient
to distinguish individuals of each species found in the LCR study
area. Photographs of <u>R</u>. <u>aurora</u> and <u>R</u>. <u>pretiosa</u> from the LCR are
seen in Figs. 8-9.

<u>R</u>. <u>aurora</u> tadpoles metamorphose at a body size of
23-27 mm. Males become sexually mature at 45 mm sv length, a
size reached during their first full year after transformation.
They breed at the start of their second full year. Males reach
a maximum of 64 mm sv length. <u>R</u>. <u>aurora</u> females are mature at
62 mm sv length which they achieve in about 4 years. They first
breed at the start of their 4th or 5th full year after trans-
formation. Females grow to a maximum size of 77-80 mm sv length.

Tadpoles of <u>R</u>. <u>pretiosa</u> transform at a sv length of
33-37 mm. Males are mature at 45 mm sv length, and they breed
at the start of their second year. Females first breed at the
start of their third year, and are mature at 62 mm sv length.
Male <u>R</u>. <u>pretiosa</u> grow to a maximum of 64 mm and females to
80-82 mm sv length.

Several features of the morphology of the frogs are
important in that the differences between the two species are
related to their divergent behavior. The hind limbs of <u>R</u>. <u>aurora</u>
are relatively longer than are those of <u>R</u>. <u>pretiosa</u>. A com-
parison of their hind limb lengths relative to body size is seen

Figure 8

Male _Rana aurora_ (top) and _Rana pretiosa_.

Figure 9

Male _Rana aurora_ (left) and _Rana pretiosa_. Note eyes of _Rana pretiosa_ face upwards.

in Fig. 10. The outstretched hind limb of R. aurora is about
twice as long as its body length, while that of R. pretiosa is
only about 1½ times as long as its body. An inspection of the
skeletons and isolated limb bones of specimens of each species
reveals that the tibio-fibula bone in the limb of R. aurora is
relatively longer than the corresponding bone in the limb of
R. pretiosa.

Another feature of the limbs that differs between the
species is the degree of webbing on the hind feet. In R. pretiosa,
the webbing is more extensive and extends nearly to the tip of
the digits of the hind feet. In R. aurora, the digits extend
beyond the webbing for at least several mm. All digits of
R. pretiosa are nearly completely joined by webbing, except for
the 4th and longest digit. Moreover, the actual digits of
R. pretiosa do not seem as muscular and thick as those of
R. aurora. The callosities on the joints of the digits are
more pronounced in the feet of R. aurora. A representation of
the hind feet of both species showing the difference in webbing
and digit development is seen in Fig. 11.

A very important distinction between the species is
the position of their eyes. Those of R. aurora face laterally,
while those of R. pretiosa face upwards. This difference can be
seen in Fig. 9.

The skin of R. pretiosa is covered with a mucus coat-
ing which is absent from R. aurora. The mucus secretion becomes
very copious when the frog is handled, and because the frog is
normally wet from immersion in water, it becomes very slippery
and difficult to hold.

Figure 10

Relative size of hind limbs of Rana aurora and Rana pretiosa. Lines fitted to least squares regression where y = hind limb length (mm) and x = snout-vent length (mm). For Rana aurora, $y = -7.8 + 2.02x$, and for Rana pretiosa, $y = 3.9 + 1.50x$.
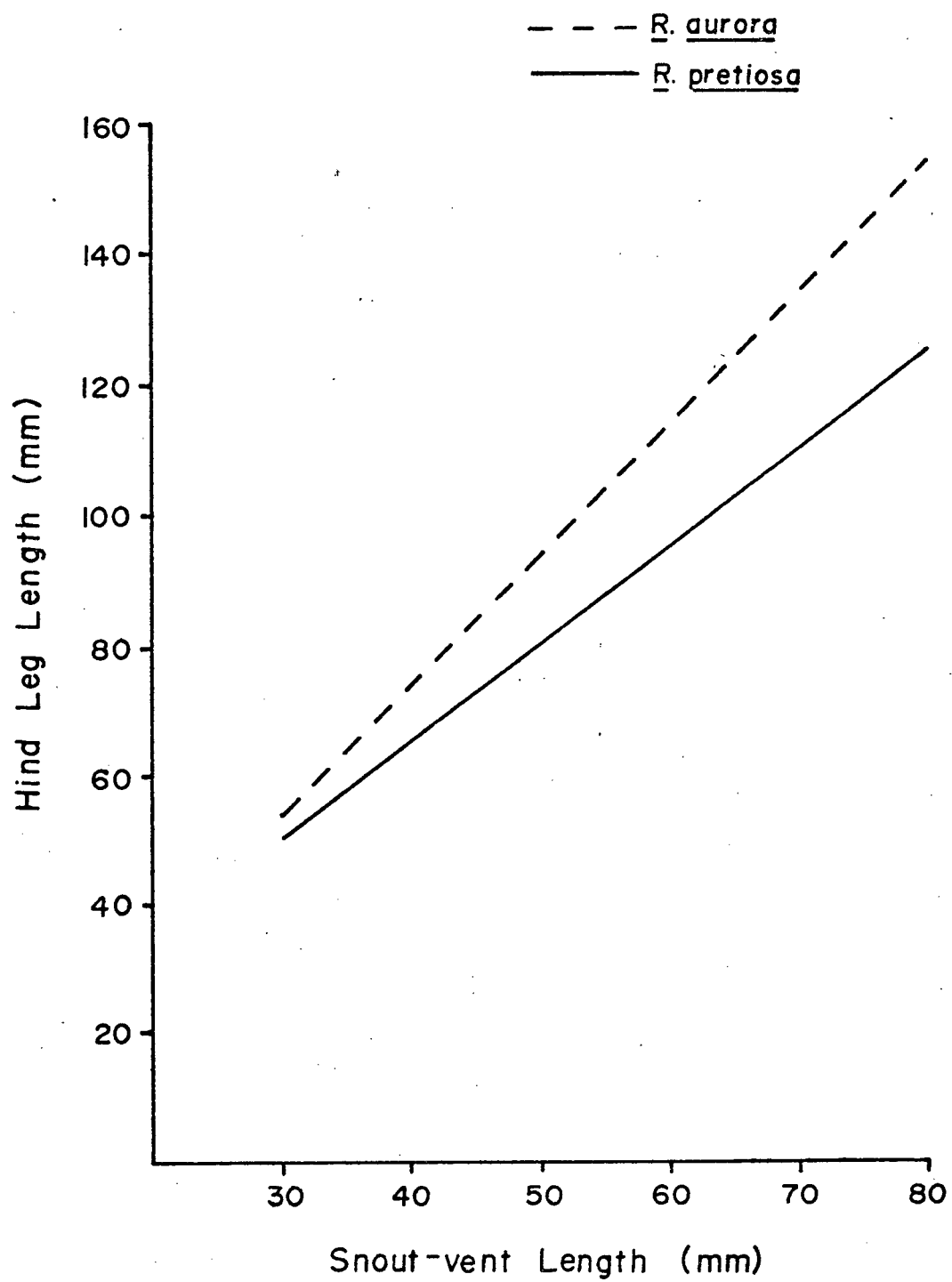
Figure 11

Dorsal view of right hind foot of *Rana aurora* and *Rana pretiosa*, based on foot of female 60 mm snout-vent length.
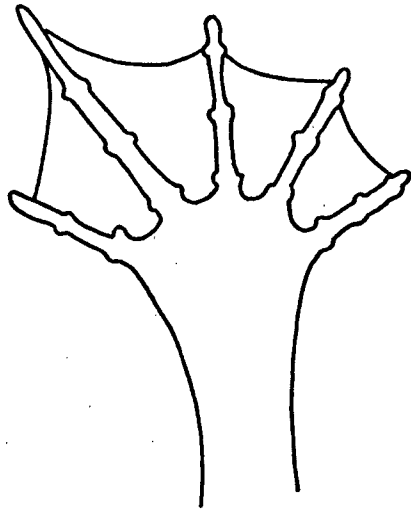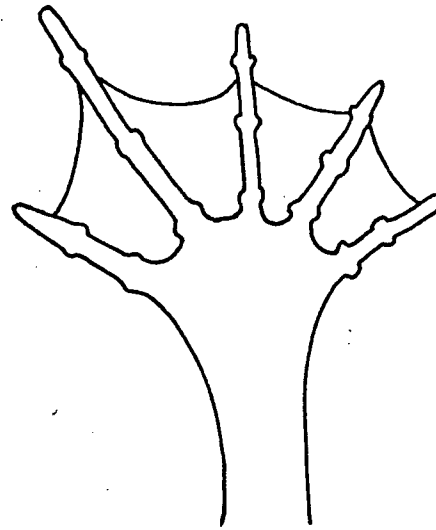
Rana pretiosa   Rana aurora

B. __Ecology__

a. __Habitat Preferences__

In the field, R. __pretiosa__ is usually found in the
water, and rarely more than a foot away from water. When rain-
pools are present in the spring, individuals sit either in the
pools or along the margins. When the rainpools dry, R. __pretiosa__
moves to the river, and none are found active in the field away
from the standing water. In the river, they sit in the shallows,
half submerged or they float in deeper water, clinging to
aquatic vegetation, often with only their head visible above
water. At times they will be on the banks of the river, only a
few inches from the water. Only on wet, rainy days does
R. __pretiosa__ move away from the vicinity of standing water.

In contrast, R. __aurora__ is nearly always found on land.
They may be near standing water, but they remain on land, and
move within tangles of vegetation near the water. They also
move many feet away from water in both dry and wet conditions.
When rainpools dry, R. __aurora__ moves either to the woods or to
the vicinity of the river. They are found on and in the vegeta-
tion along the river edge and several feet away. They do not
move into the water as do R. __pretiosa__.

During the summer of 1969, I caught 98 R. __pretiosa__.
Of these, 86 were taken in water and 12 on land only inches away
from water. Of 74 R. __aurora__ caught on the same days, 72 were on
land and 2 were in water.

The tests on habitat preferences with frogs placed in

the plastic swimming pool yielded clear results. During 15 trials of 30 minutes each (before snakes were introduced) 30 observations were made on the frogs. R. aurora was on land 27 times and in the water 3 times; R. pretiosa was on land 7 times and in water 23 times. Those R. pretiosa on land had sometimes not found water for 15-20 minutes, but once they did, they did not leave it to return to land.

b. Food

1) Feeding behavior in the field

Adult and juvenile R. aurora were rarely sighted until they began jumping as I neared them in my searches of the field. I was unable to make meaningful observations of their natural feeding behavior.

The feeding behavior of newly transformed R. aurora was more easily observed. After metamorphosis in July, the small frogs remain along the river banks. They are usually found a few feet from the river edge in patches of Ranunculus that grows along the shore. On warm dry days during the summer, they feed at the water margin, catching small insects along the banks, in the vegetation, and occasionally swimming a few inches into the river to take an insect on the water surface or on an aquatic plant. In the early part of the day when there is still moisture left on the vegetation, the small R. aurora move into the vegetation and feed in the undergrowth.

During or after a rain, small R. aurora move many feet from the river, on the carpet of Ranunculus and near Carex, trying to catch spiders and other small insects. If rainpools

form in the field, the frogs feed along the margins, stalking

small prey in and out of the water. They often remain in the

vicinity of the rainpools as long as they contain water, but

once these dry, they again return to the river margins.

Although I did not observe feeding behavior in adult

R. aurora, individuals were often scared up as I walked along

the river in the vegetation during the summer months. Presumab-

ly they were feeding in the vegetation along the river margins,

as were the young-of-the-year individuals.

R. pretiosa (young and adult) are easily observed in

their natural feeding behavior. Individuals were usually seen

from far enough away that I was able to observe them without

disturbing them.

Throughout the year, R. pretiosa feeds in or along

bodies of water, either the river, pond, or rainpools when

present. During May and early June, when rainpools are present

in the field, R. pretiosa feeds along the sides of these pools,

or while floating on the water surface. During the summer, the

frogs float in the river, hanging onto stems or other vegetation,

either in mid-stream or at the river margins. Usually they are

completely submerged except for their heads that protruded above

the water. They often remain half concealed in thick beds of

Potamogeton or Myriophyllum. Depending on the temperature of

the day, they also sit on exposed mud along the river margins,

and as the temperature rises they move into the water.

R. pretiosa remains motionless for long periods, some-

times for an hour or more. Any suitable item that moves near

them evokes an orientation response, and if the prey is close,

the frog strikes at it. Usually a prey is located on the water surface, and the frog swims towards it, kicking with the hind limbs and making little disturbance. Usually only the frog's head and eyes protrude above the water. After stalking the prey in this manner, R. pretiosa strikes from close range.

On dry days, R. pretiosa is rarely found out of water. At most it is within a foot of the water. On dry days, I saw no feeding activity on land in the vegetation; all feeding activity was in the water. However, during and after rain, these frogs move into the wet undergrowth and feed in and among the vegetation, sometimes many feet from the river. They quickly move into rainpools when these form in the field and feed from the water surface or margins.

Newly transformed frogs of both species are often seen feeding within inches of each other, usually along the river edge or near rainpools. On hot summer days, when R. aurora is restricted to the river margins, the two species often feed in close proximity. However, on such occasions, R. pretiosa is almost always in the water, while R. aurora is on the nearby land. R. aurora is more active in seeking food and moves in and out of the vegetation; R. pretiosa spends more time waiting for prey to move near.

Both species are primarily diurnal in feeding habits, but may feed at night during warm summer nights. I did not observe nocturnal activities.

I threw various food items to adult R. pretiosa to note their responses. Small grasshoppers and other small prey were readily taken if the prey were thrown near the frogs in the

water. On many occasions, a frog would seize a prey item and then quickly submerge its head to swallow. Occasionally, a frog came onto the river bank to take a prey item I had thrown, but always immediately returned to water and often submerged to swallow the food. These frogs seemed reluctant to move onto land to take food, although they often swam to shore and invest-igated food items thrown onto shore.

Adult R. pretiosa seized and ate adult treefrogs, Hyla regilla (30-35 mm sv length), and small R. aurora and R. pretiosa (25-35 mm sv length). Three times, without any manipulation on my part, I saw adult R. pretiosa grab and attempt to swallow newly metamorphosed R. aurora. In two of these cases, the R. pretiosa swallowed the prey, the third frog escaped by strugg-ling violently. Adult R. pretiosa often oriented to small R. aurora moving on land, but they did not leave the water.

In laboratory terraria, adult R. aurora differ from adult R. pretiosa in an obvious way. R. aurora readily jumps a foot or more in attempting to grab a prey item; it is usually accurate in its jumps. R. pretiosa seldom jumps, but moves slow-ly towards a prey item and grabs it directly, or jumps from a few inches away. It sometimes jumps many times in succession at a prey, and often tripped over its own feet in its awkward jumping motions.

2) Analysis of stomach contents

From May to October 1968, 104 R. aurora and 41 R. pretiosa were collected and their gut contents analyzed for food items. The sample of each was separated into 2 categories:

78 newly transformed R. aurora; 26 juvenile-adult R. aurora;
18 newly transformed R. pretiosa; 23 juvenile-adult R. pretiosa.
Newly metamorphosed frogs first appear in samples taken in July
and August. This is the time that they first begin transforming
from tadpoles to frogs.

The stomach and intestinal tract of every frog in all
samples contained some food item; there were no empty stomachs.

Because I did not survey the invertebrates in the
marshes where the frogs were caught, I have no estimates of
availability and abundance of prey. Therefore no data are
available on whether the frogs show food preferences. However,
other studies of ranid feeding behavior (Turner 1958, Jenssen
and Klimstra 1966) indicate frogs feed on what is available at
any specific time, and definite food preferences are unknown.
For example, arachnids are available in all months from May to
October, and appear in the guts of both species during each
monthly collection. But syrphid flies and larvae first become
abundant in the guts in July and August, the time period when
they are especially abundant in the marshes.

The food taken by all R. aurora is listed in Table I,
and the food eaten by all R. pretiosa in Table II. Food items
found in the guts of newly metamorphosed R. aurora and juvenile-
adult R. aurora are listed in Tables III and IV. Tables V and
VI list the same data for newly metamorphosed R. pretiosa and
juvenile-adult R. pretiosa. The data presented in these tables
are the percentage of all stomachs within the sample containing
a particular food item, and the percentage of all the food eaten
made up by that particular food item.

The number of food classifications and the percentage overlap of these food classifications between and within the samples of each species is seen in Table VII. Of special interest is that the newly metamorphosed frogs of both species have the highest percentage overlap with other samples. Newly metamorphosed R. pretiosa share as much as 73.1% of the food they exploit with newly metamorphosed R. aurora and juvenile-adult R. pretiosa.

Another means of judging the degree to which both species, and age groups within species, share the same resources is to examine the dominant foods appearing in their gut contents. If foods that are used frequently by each species are shared, then food overlap may be an important aspect of possible competition between the species. The dominant foods were determined in two fashions. First, the top food classes were selected on the basis of frequency in the stomach samples. Second, the top food classes were selected on the basis of their abundance in the stomach samples. The top eight food items for each sample were compiled by both techniques.

The top eight foods based on their abundance in the guts of frogs in the different samples make up most of the food eaten. For all R. aurora, the top eight foods comprise 71.4% of all the food, and for all R. pretiosa, the top eight comprise 57.3% of all the food items. For size classes within species, the dominant eight foods make up the following percentages of all food eaten: newly metamorphosed R. aurora - 72%, Juvenile-adult R. aurora - 76%, newly metamorphosed R. pretiosa - 74%, juvenile-adult R. pretiosa - 55.5%.

A comparison of the percentage overlap of the dominant eight food classes based on their frequency occurrence is listed in Table VIII. Table IX compares the percentage overlap of the dominant eight foods based on their abundance in all the stomachs within a sample. The value 75% in Table VIII is striking. This means that newly metamorphosed frogs of both species share 75% of their most commonly eaten foods. Furthermore, they share 60.2% of the prey items that they eat in greatest numbers (Table IX). If the samples within each species are combined, then the species share 87.5% of the dominant foods occurring in most stomachs (Table VIII), and 75% of the foods eaten in most abundance (Table IX).

The overlap in diet between the combined samples of each species, based on the dominant eight foods, is illustrated in Figs. 12 and 13. Figs. 14 and 15 illustrate the overlap in dominant foods of different age classes of frogs. (Note that the actual food items, classified to family for most, are listed in Figs. 12-15).

The food items among the dominant prey taken which are not shared reveal important differences in the diet and feeding behavior of the two species, especially between the newly trans-formed individuals. R. aurora feed heavily on land slugs that are available away from the water in the vegetation and mud. These slugs appear only sparsely in the stomachs of R. pretiosa. In contrast, small R. pretiosa eat large numbers of Dolichopodidae, an aquatic dipteran. This aquatic prey is not taken by R. aurora.

3) Laboratory feeding tests

The results of feeding tests with newly metamorphosed

TABLE I

Analysis of food items in gut contents of 104 newly metamorphosed and juvenile-adult Rana aurora

Food items	% of all stomachs	% of total food items	Food items	% of all stomachs	% of total food items
Mollusca			Insecta		
Snail	3.8	1.5	Trichoptera	3.8	.6
Slug	18.3	4.0	Trichoptera larvae	1.9	.4
Arachnida	51.0	15.6	Lepidoptera		
Insecta			Geometridae larvae	1.0	.1
Orthoptera			Noctuidae larvae	2.9	.4
Locustidae	1.0	.1	Diptera		
Plecoptera	1.0	.1	Tipulidae	2.9	.4
Hemiptera			Tipulidae larvae	2.9	.6
Gerridae	2.9	.4	Chironomidae larvae	8.7	2.4
Nabidae	6.7	1.1	Cecidomyiidae	1.0	.1
Saldidae	6.7	1.1	Mysetopliidae	1.9	.3
Miridae	1.0	.1	Otitidae	1.0	.1
Cercopidae	41.3	17.6	Stratiomyidae larvae	1.0	.1
Cicadellidae	17.3	6.6	Dolichopodidae	5.8	1.9
Aphididae	13.5	4.6	Ephydridae	3.8	.8
Coleoptera			Syrphidae larvae	25.0	7.5
Carabidae	26.0	7.5	Canopidae	1.0	.1
Carabidae larvae	4.8	1.2	Bibionidae	1.0	.1
Dytisicidae	1.0	.1	Trupaneidae	1.9	.4
Limnebiidae	4.8	.8	Muscidae	1.9	1.0
Staphylinidae	26.9	8.0	Borboridae	2.9	.4
Staphylinidae larvae	1.9	.4	Hymenoptera		
Phalacridae	1.9	.3	Tenthredinidae	1.9	.3
Coccinellidae	1.0	.1	Tenthredinidae larvae	2.9	.4
Lampyridae larvae	1.0	.1	Ichneumonidae	12.5	3.6
Elateridae larvae	1.0	.1	Braconidae	1.0	.1
Scarabaeidae	1.9	.4	Chalcididae	1.9	.6
Chrysomelidae	8.7	1.8	Cynipidae	2.9	.4
Mylabridae	1.0	.1	Trichogrammatidae	1.0	.1
Curculionidae	5.8	1.1	Formicidae	8.7	1.2
			Total		100

TABLE II

Analysis of food items in gut contents of 41 newly metamorphosed and juvenile-adult Rana pretiosa.

Food items	% of all stomachs	% of total food items	Food items	% of all stomachs	% of total food items
Mollusca			Coleoptera		
Snail	4.9	1.3	Nitidulidae	2.4	.7
Slug	2.4	.3	Scarabaeidae	2.4	.3
Arachnida	22.0	8.5	Chrysomelidae	12.2	9.1
Insecta			Chrysomelidae larvae	2.4	2.3
Orthoptera			Curculionidae	12.2	1.6
Locustidae	2.4	.3	Trichoptera adult	2.4	.3
Odonata			Trichoptera larvae	2.4	.3
Coenagrionidae	4.9	.7	Lepidoptera		
Hemiptera			Hepialidae larvae	2.4	.3
Corixidae	2.4	.3	Noctuidae larvae	2.4	.3
Corixidae nymphus	2.4	.3	Pieridae larvae	2.4	.3
Gerridae	9.8	2.6	Diptera		
Nabidae	9.8	1.6	Tipulidae	4.9	1.0
Saldidae	9.8	1.3	Chironomidae larvae	2.4	.3
Cercopidae	17.1	6.2	Cecidomyiidae	4.9	.7
Cicadellidae	12.2	5.5	Lauxaniidae	4.9	.7
Aphididae	17.1	3.3	Dolichopdidae	22.0	7.8
Coleoptera			Ephydridae	7.3	1.3
Carabidae	19.5	7.8	Syrphidae adult	2.4	.7
Carabidae larvae	2.4	.7	Syrphidae larvae	17.1	6.5
Dytiscidae	12.2	1.6	Bibionidae	4.9	1.6
Staphylinidae	17.1	5.9	Tachnidae	7.3	1.6
Hydrophilidae larvae	2.4	.3	Hymenoptera		
Coccinellidae	4.9	.7	Ichneumonidae	4.9	.7
Coccinellidae larvar	4.9	1.0	Vespidae	14.6	2.3
Cantharidae	2.4	.3	Formicidae	22.0	4.6
Heteroceridae	2.4	.7	Bombidae	2.4	.3
Buprestidae	7.3	1.3	Apidae	7.3	1.6
Haliplidae	2.4	.3			
Meloidae	2.4	.7	Total		100

TABLE III

Analysis of food items in gut contents of 78 newly metamorphosed _Rana aurora._

Food items	% of all stomachs	% of total food items	Food items	% of all stomachs	% of total food items
Mollusca			Diptera		
Snail	3.8	1.8	Tipulidae adult	1.3	.2
Slug	23.1	5.2	Tipulidae larvae	3.8	.7
Arachnida	48.7	12.0	Chironomidae larvae	11.5	3.1
Insecta			Cecidomyiidae	1.3	.2
Orthoptera			Mysetopliidae	2.6	.4
Locustidae	1.3	.2	Otitidae	1.3	.2
Plecoptera	1.3	.2	Stratiomyiidae larvae	1.3	.2
Hemiptera			Dolichopodidae	6.4	2.3
Gerridae	1.3	.2	Ephydridae	5.1	1.4
Nabidae	5.1	.7	Syrphidae larvae	32.1	7.5
Saldidae	6.4	1.1	Trupaneidae	2.6	.6
Cercopidae	52.6	22.9	Muscidae	1.3	.2
Cicadellidae	17.9	7.7	Borboridae	3.8	.6
Aphididae	16.7	5.7	Hymenoptera		
Coleoptera			Tenthredinidae	1.3	.2
Carabidae adult	16.7	4.1	Tenthredinidae larvae	3.8	.6
Carabidae larvae	3.8	1.3	Ichneumonidae	14.1	4.1
Dytiscidae	1.3	.2	Braconidae	1.3	.2
Staphylinidae	20.5	6.5	Chalcididae	2.6	.7
Staphylinidae larvae	2.6	.6	Cynipidae	3.8	.6
Phalacridae	2.6	.4	Formicidae	10.3	1.5
Elateridae larvae	1.3	.2	Total		100
Scarabaeidae	2.6	.6			
Chrysomelidae	7.7	1.8			
Curculionidae	2.6	.4			
Trichoptera adult	2.6	.4			
Trichoptera larvae	1.3	.2			
Lepidoptera					
Noctuidae larvae	1.3	.2			

TABLE IV

Analysis of gut contents of 26 juvenile-adult Rana aurora.

Food items	% of all stomachs	% of total food items	Food items	% of all stomachs	% of total food items
Mollusca			Coleoptera		
Snail	3.8	.6	Chrysomelidae	11.5	1.7
Slug	3.8	.6	Mylabridae	3.8	0.6
Arachnida	57.7	26.7	Curculionidae	15.4	3.3
Insecta			Tricoptera adult	7.7	1.1
Hemiptera			Tricoptera larvae	3.8	1.1
Gerridae	7.7	1.1	Lepidoptera		
Nabidae	11.5	2.2	Geometridae larvae	3.8	0.6
Saldidae	7.7	1.1	Noctuidae larvae	7.7	1.1
Miridae	3.8	.6	Diptera		
Cercopidae	7.7	1.7	Tipulidae	7.7	1.1
Cicadellidae	15.4	3.3	Dolichopodidae	3.8	1.1
Aphididae	3.8	1.1	Syrphidae larvae	3.8	6.1
Coleoptera			Canopidae	3.8	0.6
Carabidae adult	53.8	17.8	Bibionidae	3.8	0.6
Carabidae larvae	7.7	1.1	Muscidae	3.8	3.3
Limnebiidae	19.2	3.3	Hymenoptera		
Staphylinidae	46.2	12.8	Tenthredinidae	3.8	0.6
Coccinellidae	3.8	0.6	Ichneumonidae	7.7	1.1
Lampyridae larvae	3.8	0.6	Trichogrammatidae	3.8	0.6
			Formicidae	3.8	0.6
			Total		100

TABLE V

Analysis of gut contents of 18 newly metamorphosed _Rana pretiosa_

Food items	% of all stomachs	% of total food items	Food items	% of all stomachs	% of total food items
Arachnida	77.8	14.7	Lepidoptera		
Insecta			Noctuidae larvae	5.6	.9
Hemiptera			Diptera		
Gerridae	5.6	.9	Chironomidae larvae	5.6	.9
Nabidae	11.1	1.7	Cecidomyiidae	11.1	1.7
Saldidae	11.1	1.7	Dolichopodidae	22.2	13.8
Cercopidae	27.8	14.7	Ephydridae	5.6	1.7
Cicadellidae	16.7	12.9	Syrphidae larvae	22.2	3.4
Aphididae	22.2	4.3	Tachnidae	5.6	.9
Coleoptera			Hymenoptera		
Carabidae	11.1	4.3	Ichneumonidae	5.6	.9
Dytisicidae	11.1	1.7	Vespidae	5.6	.9
Staphylinidae	16.7	3.4	Formicidae	16.7	6.0
Coccinellidae	11.1	1.7			
Coccinellidae larvae	5.6	.9	Total		100
Heteroceridae	5.6	1.7			
Nitidulidae	5.6	1.7			
Chrysomelidae	5.6	1.7			
Curculionidae	5.6	.9			

TABLE VI

Analysis of gut contents of 23 juvenile-adult _Rana_ _pretiosa._

Food items	% of all stomachs	% of total food items	Food items	% of all stomachs	% of total food items
Mollusca			Coleoptera		
Snail	8.7	2.1	Buprestidae	13.0	2.1
Slug	4.3	.5	Haliplidae	4.3	.5
Arachnida	21.7	4.7	Meloidae	4.3	1.0
Insecta			Scarabaeidae	4.3	.5
Orthoptera			Chrysomelidae adult	17.4	13.6
Locustidae	4.3	.5	Chrysomelidae larvae	4.3	3.7
Odonata			Curculionidae	17.4	2.1
Coenagrionidae	8.7	1.0	Tricoptera adult	4.3	.5
Hemiptera			Tricoptera larvae	4.3	.5
Corixidae adults	4.3	.5	Lepidoptera		
Corixidae nymphs	4.3	.5	Hepialidae larvae	4.3	.5
Gerridae	13.0	3.7	Pieridae larvae	4.3	.5
Nabidae	8.7	1.6	Diptera		
Saldidae	8.7	1.0	Tipulidae	8.7	1.6
Cercopidae	8.7	1.0	Lauxaniidae	4.3	1.0
Cicadellidae	8.7	1.0	Dolichopodidae	21.7	4.2
Aphididae	13.0	2.6	Ephydridae	8.7	1.0
Coleoptera			Syrphidae adult	4.3	1.0
Carabidae adult	26.1	9.9	Syrphidae larvae	13.0	8.4
Carabidae larvae	4.3	1.0	Bibionidae	8.7	2.6
Dytiscidae	13.0	1.6	Tachnidae	8.7	2.1
Staphylinidae	17.4	7.3	Hymenoptera		
Hydrophilidae larvae	4.3	.5	Ichneumonidae	4.3	.5
Coccinellidae larvae	4.3	1.0	Vespidae	21.7	3.1
Cantharidae	4.3	.5	Formicidae	26.1	3.7
			Bombidae	4.3	.5
			Apidae	13.0	2.6
			Total		100

TABLE VII

Percentage overlap of total food classifications between species and age groups within species.

		Rana aurora		Rana pretiosa	
		Newly meta-morphosed	Juvenile-adult	Newly meta-morphosed	Juvenile-adult
Number of food classes		45	33	26	43
Percentage overlap of food classes of group above with group below					
Rana aurora	Newly meta-morphosed	-	69.7	73.1	55.8
	Juvenile-adult	51.1	-	65.4	48.8
Rana pretiosa	Newly meta-morphosed	42.2	51.5	-	44.2
	Juvenile-adult	53.3	63/6	73.1	-

TABLE VIII

Percentage overlap of dominant eight food items (those food items occurring in most frog stomachs).

Group on right overlaps with group below		*Rana aurora		*Rana pretiosa	
		Newly metamorphosed	Juvenile-adult	Newly metamorphosed	Juvenile-adult
Rana aurora	Newly metamorphosed	–	37.5	75	37.5
Rana aurora	Juvenile-adult	50	–	50	60.2
Rana pretiosa	Newly metamorphosed	75	50	–	50
Rana pretiosa	Juvenile-adult	37.5	60.2	60.2	–

* All Rana aurora combined and all Rana pretiosa combined share 87.5% of dominant eight foods.

TABLE IX

Percentage overlap of dominant eight food items (those food items most abundant in all stomachs).

Group on right over-laps with group below		*Rana aurora		*Rana pretiosa	
		Newly meta-morphosed	Juvenile-adult	Newly meta-morphosed	Juvenile-adult
Rana aurora	Newly meta-morphosed	–	60.2	60.2	50
	Juvenile-adult	60.2	–	60.2	50
Rana pretiosa	Newly meta-morphosed	60.2	37.5	–	50
	Juvenile-adult	50	50	50	–

* All Rana aurora combined and all Rana pretiosa combined share 75% of dominant eight foods.

o

Figure 12

Overlap of dominant food items of all <u>Rana</u> <u>aurora</u> and all <u>Rana</u> <u>pretiosa</u>, and percentage of total stomachs which contained the food. Top eight food items are those appearing in most stomachs. Number in parentheses is total number of stomachs for each group.

Per Cent of Stomachs Containing Item

Food Item

Arachnida
Cercopidae
Staphylinidae
Carabidae
Syrphidae larvae
Aphididae
Cicadellidae
Slugs
Dolichopodidae
Formicidae

☐ R. aurora (n=104)
▨ R. pretiosa (n = 41)
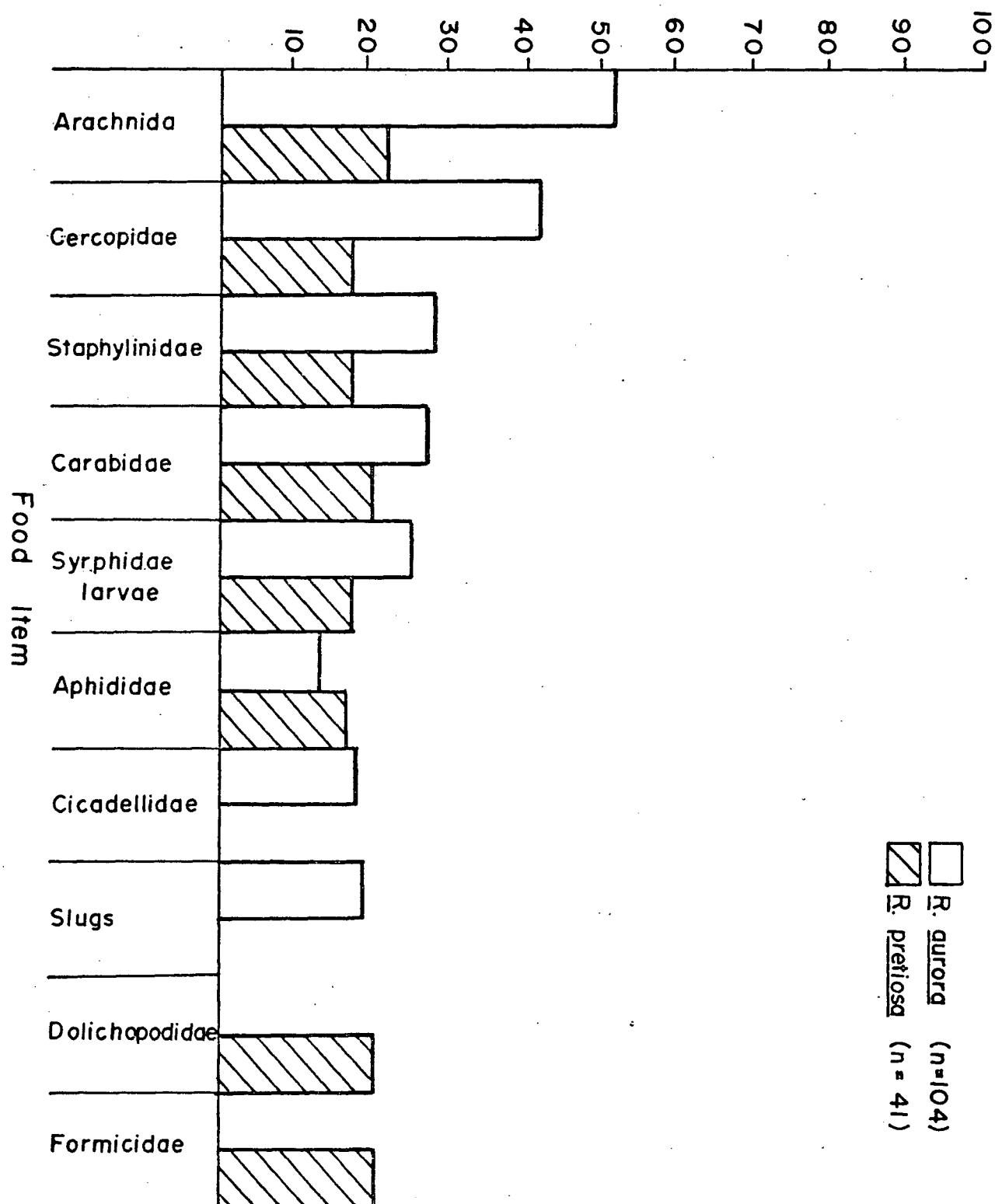
Figure 13

Overlap of dominant food items of all <u>Rana</u> <u>aurora</u> and all <u>Rana</u>
<u>pretiosa</u> and percentage of total food intake each food item
comprises. Top eight food items are those most abundant in all
stomachs of each species. Number in parentheses is total number
of food items in all samples.

Per Cent of total Food Items

100
90
80
70
60
50
40
30
20
10

R. aurora (722 items)
R. pretiosa (307 items)

Arachnida
Cercopidae
Staphylinidae
Carabidae
Syrphidae larvae
Cicadellidae
Aphididae
Slugs
Chrysomelidae
Dolichopodidae
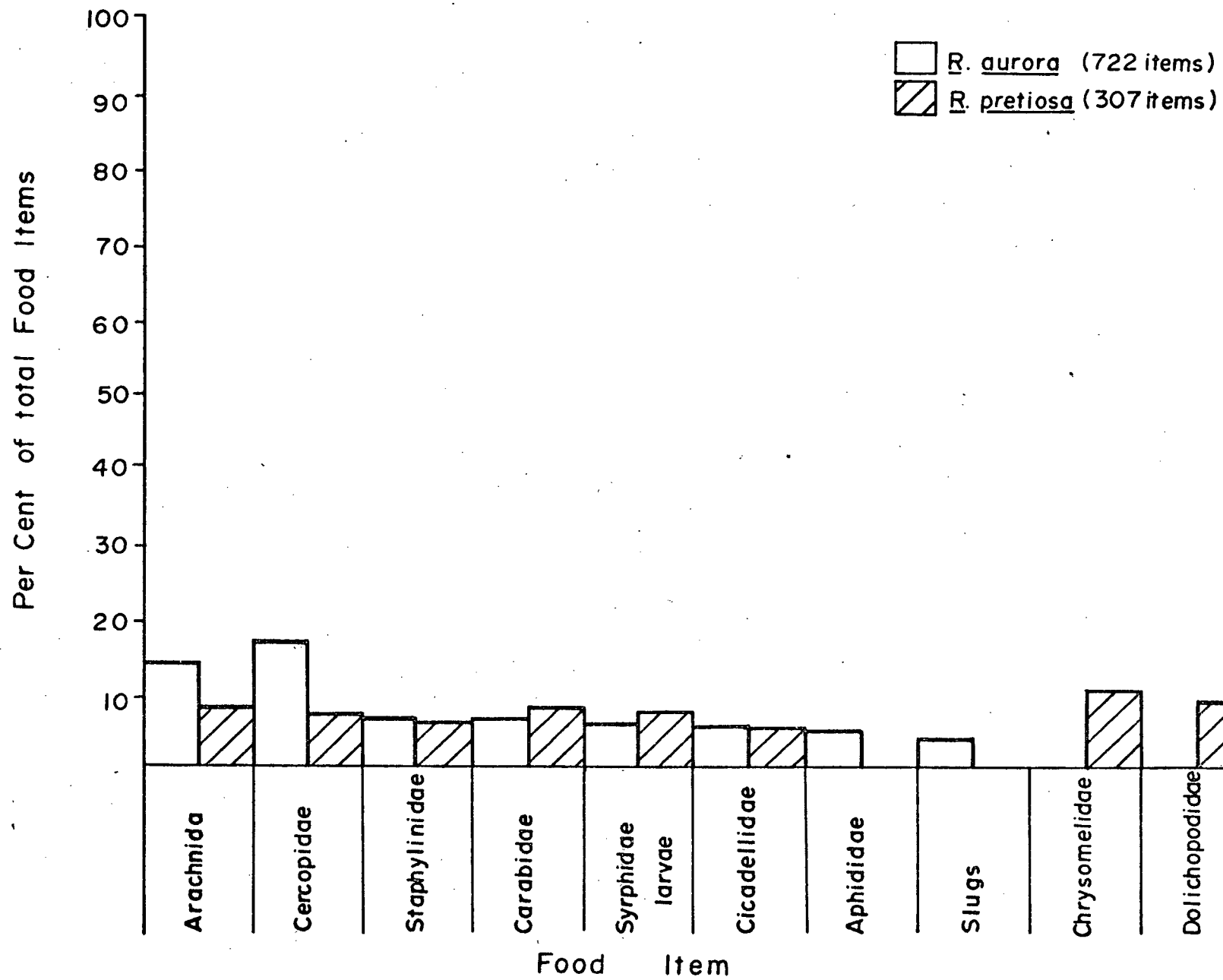
Food   Item

Figure 14

Overlap of dominant food items of frogs of different age classes. Top eight items for each age class are those appearing in most stomachs within each class. Number in parentheses is total number of stomachs for each age class.

Per Cent of Stomachs Containing Item

Legend:
- Juvenile–Adult *R. aurora* (n=26)
- Juvenile–Adult *R. pretiosa* (n=23)
- Newly Metamorphosed *R. aurora* (n=78)
- Newly Metamorphosed *R. pretiosa* (n=18)

Y-axis: 10, 20, 30, 40, 50, 60, 70, 80, 90, 100

Food Item (X-axis):
Arachnida, Staphylinidae, Carabidae, Cicadellidae, Chrysomelidae, Curculionidae, Limnebiidae, Nabidae, Dolichopodidae, Formicidae, Vespidae, Cercopidae, Syrphidae larvae, Slugs, Aphididae

Figure 15

Overlap of dominant food items of frogs of different age classes.
Top eight items are those most abundant in all stomachs of each
age class. Number in parentheses is total number of food items
of all kinds found in stomachs of each group.

Per Cent of Total Food Items

Food Item

Arachnida
Carabidae
Staphylinidae
Syrphidae larvae
Cicadellidae
Curculionidae
Limnebiidae
Muscidae
Dolichopodidae
Formicidae
Gerridae
Cercopidae
Aphididae
Slugs
Chrysomelidae

Juvenile-Adult R. aurora (180 items)
Juvenile-Adult R. pretiosa (191 items)
Newly Metamorphosed R. aurora (542 items)
Newly Metamorphosed R. pretiosa (116 items)
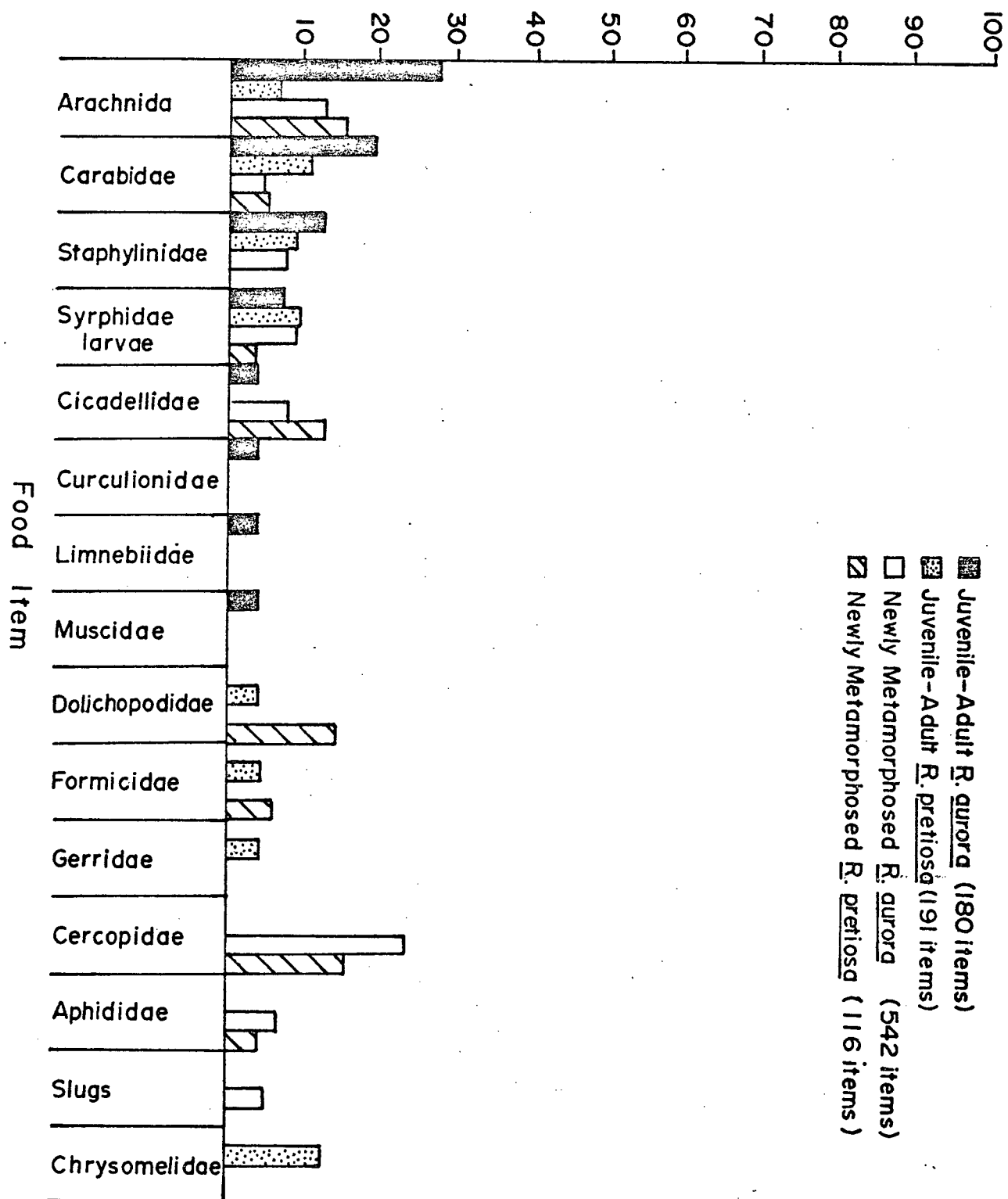
frogs under wet and dry conditions are seen in Table X. The total number of strikes, the percentage of successful strikes, and the actual numbers of flies eaten, are listed. The results under each of the two conditions were pooled, and the differences between species tested by Chi squares; the levels of significance for differences observed are seen in Table XI.

In both wet and dry conditions, R. pretiosa attempted to capture flies more frequently than did R. aurora. R. pretiosa orients and strikes as long as flies are present. When they see a fly, they move to within an inch or less and strike at it. R. pretiosa usually misses the first strike, and may strike many times in succession until the fly is either caught or moves away. In wet bowls, R. pretiosa ate and struck almost exclusively at flies on the water surface, and seldom attempted to eat flies on the walls of the bowls. In contrast, R. aurora rarely strikes at flies on the water surface in wet bowls, but tries for those prey that are moving on the walls and cover of the bowls. R. aurora jumps at the flies from several inches away, and is usually successful. If not, they jump two or three times in quick succession, but not repeatedly as did R. pretiosa. In the dry bowls, R. aurora is very accurate and usually catches the flies on their first attempt.

Although R. pretiosa is more active at striking at flies, and does so without hesitating before each strike (R. aurora characteristically hesitates before striking), they are no more successful at capturing flies than R. aurora. The percentage of successful strikes for both species does not differ under each of the conditions, although R. pretiosa spends much

TABLE X

Total number of strikes, percentage of strikes which were
successful, and number of flies actually eaten in wet and
dry conditions by Rana aurora and Rana pretiosa.

| | Wet | | Dry | |
	Rana aurora	Rana pretiosa	Rana aurora	Rana pretiosa
Total number of strikes	171	476	268	428
Percentage of strikes successful	25.6	25.1	38.6	42.1
Number of flies actually eaten	39	118	102	178

TABLE XI

Probabilities associated with differences in feeding efficiency
of Rana aurora and Rana pretiosa under wet and dry conditions.

Total number of strikes	Percentage of strikes successful	Number of flies actually eaten
R. aurora wet – R. pretiosa wet*	R. aurora wet – R. pretiosa wet	R. aurora wet – R. pretiosa wet*
R. aurora dry – R. pretiosa dry*	R. aurora dry – R. pretiosa dry	R. aurora dry – R. pretiosa dry*
R. aurora wet – R. aurora dry*	R. aurora wet – R. aurora dry	R. aurora wet – R. aurora dry*
R. pretiosa wet – R. pretiosa dry*	R. pretiosa wet – R. pretiosa dry*	R. pretiosa wet – R. pretiosa dry*

* indicates P < .05 for differences observed.

more effort at feeding than does R. aurora. However, R. pretiosa eats more flies since it strikes more often than R. aurora.

Both species are more successful at capturing flies in dry conditions than in wet, but they do not differ in their abilities in dry conditions. In the wet bowls, R. pretiosa attempts to capture flies that are water bound, but with each lunge toward a fly, the frog pushes the water and thus moves the fly. However, they strike repeatedly, and are usually ultimately successful. R. aurora is less accurate in its jumping ability in wet bowls, since it still attempts to capture flies on the walls and not those in the water.

4) Starvation experiments

Starvation tests with newly metamorphosed frogs showed that they are able to live for many days on the energy source retained from their life as tadpoles.

Of the initial ten newly transformed R. aurora, six lived from 38-45 days (mean of 42 days) before starving. The remaining four were given food after 45 days, but three of them died from three to five days later. One surviving frog lived well and grew although it had been starved for 45 days.

Five of the initial ten R. pretiosa lived from 31-35 days (mean of 33.8 days) before dying. After 35 days the remaining five were fed flies in abundance, but four died from one to four days later. The lone survivor regained a normal healthy appearance and fed well thereafter.

Individuals of both species that survived without food until food was given to them were weak and emaciated. How-

ever, when flies were added to the bowls with the frogs, all
individuals attempted to feed. All except one of each species
was too weak to feed efficiently, and although some did catch
food, they were beyond the point of survival.

c. Temperature

1) Field and frog temperatures

In the Lower Fraser Valley and the LCR study area,
weather conditions in early spring of 1969 were very different
from those of the same period in 1968. A prolonged cold wave
(setting a 50-year record) in 1969 kept the river and field
under ice until late February, and freezing temperatures occurred
almost nightly until the second week of March. The air and
water temperatures which existed during the last week of
February in 1968 were not encountered until the second week of
March in 1969. The onset of breeding by both species was
delayed for almost two weeks in 1969, a fact which provides
evidence that there exists temperature thresholds necessary for
initial breeding activity.

As soon as the ice and snow melt from the spawning
sites, during February and March, both R. aurora and R. pretiosa
breed. During breeding activities, R. aurora had cloacal
temperatures as low as 6 C, but the lowest recorded for
R. pretiosa was 8.1 C. On near freezing nights, R. aurora may
remain active because they spawn while completely submerged
under water. R. pretiosa spawn at the water surface, and their
breeding activity is restricted to warmer nights when temper-
atures are above 7 C. Most R. pretiosa spawn during the day-

light hours, usually in full sunshine when air temperatures are at least 10 C.

No juvenile frogs of either species were seen active during the breeding season. Young frogs were first found about 2-3 weeks after breeding ended. By this time air temperatures had risen considerably and there were no longer freezing nights. Lowest temperatures were usually above 7 C at night, and daytime recordings began to reach 15-20 C. On days below 8-10 C, frogs were inactive.

After breeding finished, adult frogs disappeared and were not seen for about 3 weeks. The reappeared about the same time that the juveniles became active (when daily temperatures were above 10 C). By mid-April in all years, frogs of both species and all sizes had commenced regular non-breeding activities.

Cloacal temperatures of frogs were recorded at indefinite intervals from mid-April to November (the time when frogs went into hibernations). Their body temperatures were measured under a variety of climatic conditions.

Both species were inactive at temperatures below 8-10 C. In April, by dusk, air temperatures were at this minimum and frogs were inactive as I searched for them. Early morning searches in April were successful only after the air had warmed to about 10 C.

The onset of hibernation seems to be governed in part, by the low temperatures prevailing in November. In all years, frogs were not easily found in November, after a period of low temperatures. In 1968, during the last days of October, night

temperatures had dropped to 3-4 C for about 3 days, and daytime temperatures barely reached 10 C. After this cold spell, frogs were not found. An occasional frog was active on sunny days in November, but the population as a whole had hibernated.

Throughout the study, I recorded the cloacal temperatures of 115 R. aurora. These averaged 19.5 (range 9.6-28.5, SD=4.9). The cloacal temperatures of 133 R. pretiosa averaged 20.8 C (range 9.6-29.0. SD=5.0). (These temperatures are of nonbreeding frogs only). The difference between their temperatures is significant (P>.01).

On many occasions it appeared that the frogs used behavioral traits (moving into or out of direct sun, or into or out of water) as a means of controlling their body temperatures. For example, on a warm morning in June 1968, an adult female R. pretiosa was sitting on a log along the river bank. The sunshine was directly on the frog when the air temperature was 24.6 C; the frog's body temperature was undoubtedly higher. Soon the frog moved along the log until it was in the shade created by overhanging vegetation. In 10 minutes it was again in direct sunshine, and after about 5 minutes, it again moved to shade on the log. This happened three times until eventually the frog jumped into the river. I immediately caught the frog and its temperature was 27.6 C. The air temperature 2 cm above the log where the frog had been was 29.7 C, and had the frog remained in full sunshine, its temperature may have been higher.

During mid-summer, in the mornings, when the sun is shining and the air about 20 C, R. pretiosa is most often found along the river margin, at the water edge or on the mud bank,

basking in the sun. The water in the shallows is usually 3-6 C higher than in mid-stream. By afternoon, when the air rises to 25 C or more, and the river shallows reach the same temperature, R. pretiosa moves into the depths and is almost completely submerged in the cooler waters.

R. aurora uses the shade offered by vegetation in the field or along the river margin, to behaviorally thermoregulate. In the mornings, during the summer, R. aurora occurs in the open grass areas or along the exposed river banks in full sunlight. As the temperature rises to above 25 C, R. aurora is no longer found exposed to direct sun, but moves into the shade under vegetation. The temperatures in such vegetational areas is often 5 C or more lower than the exposed air.

During mid-summer, in July and August, on days with high air and water temperatures, the frogs had an opportunity to attain high body temperatures. On these days, the cloacal temperatures of the frogs are good indicators of the body temperatures they naturally prefer during their daily activities. The temperatures available in the field may be considered as a gradient, and frogs can attain their preferred temperatures by moving into the most suitable conditions. The frogs used the available heat only to a given limit. For example, on 22 May 1969, at 1000 hrs, the air in direct sunlight was 26.2 C, and the shallow water of the river was 21.4 C. Four R. pretiosa on the river bank had body temperatures of 27.3 C, and four others in the river shallows were at 24-25 C. By 1400 hrs, the air was 31.8 C in the sun, and the water was 28.2 C. Five R. pretiosa had body temperatures of 28.5 C, and three others

were from 26-27.2 C. All were in the water and not on land where they could have achieved much higher body temperatures. Eight other R. pretiosa were seen in water; none were seen on land in direct sunlight.

Similar behavior (avoidance of high temperatures) was also demonstrated by R. aurora. However, this species uses the shade within tangles of vegetation on land rather than water to regulate their body temperatures. On 9 June 1969, the air in open sun was 33.5 C. Nine R. aurora were caught in tangles of vegetation with temperatures of 24-27.5 C. No R. aurora were seen exposed in direct sunlight that day.

A clear demonstration of behavioral thermoregulation by R. aurora occurred on 2 July 1968. Only scattered pools remained from the rapidly drying pond. In these pools there were newly metamorphosed frogs as well as tadpoles about to transform. The area around the pools was open and exposed to direct sunlight. At 0900 hrs, the water temperature on the surface of the pools was 27.5 C, and about 4 inches below the surface it was 21 C, in the vegetation that choked the pool. Many R. aurora about to transform were on the water surface on the vegetation; some were at the margins of the pools. I left these frogs undisturbed and returned at 1400 hrs. This time the water surface was 34.5 C, and 4 inches below it was 26.7 C. No R. aurora were seen on the water surface or along the margins of the pools. As I sat and watched, individual R. aurora would suddenly emerge from the depths of the pools, swallow air and soon submerge again into the pools. They were staying in the cooler water in the bottom of the pools in the vegetation. As

indicated below, they could tolerate the surface temperatures only briefly, for 34.5 C is within their lethal temperature range.

At the time I measured the cloacal temperatures of frogs in the field, I also recorded the air and water temperatures, depending on where the frog was caught. The field and frog temperatures were taken within seconds of each other in an attempt to record even a small difference if it existed. Comparisons of cloacal and substrate (air or water) temperatures are made in Table XII. Table XIII lists the number of degrees difference between frog and air or water temperature.

The highest recording for R. pretiosa in air (that is, when the frog is on land and not in water) was 28.8 C. However, this maximum may be somewhat lower than the true upper limit because it is difficult to catch R. pretiosa on land on very hot days when it is usually in the water. When I did catch it on land, I often was not able to quickly record its temperature. The frogs were very active and movements lowered their temperatures by evaporative cooling.

Table XII clearly demonstrates that the body temperatures of both species are, on the average, higher than the medium (air or water) they are taken from. However, in some instances listed in Table XIII, the cloacal temperature was below that of the air or the water. This happened when the frog was in wet grasses on land. As the frog moved to escape, air cooling of its skin probably lowered its internal temperature. If a frog was caught in the shade, the body temperature was

TABLE XII

Comparisons of frog cloacal temperature (C) with temperatures
of air and water where caught.

Rana aurora

N	Cloacal	Air	Water	Probability
75	18.6 (SD=4.4)	17.2 (SD=4.9)		P < .01
37	21.1 (SD=5.2)	—	21.0 (SD=6.3)	P > .05

Rana pretiosa

| 48 | 18.8 (SD=4.7) | 17.1 (SD=4.5) | — | P < .05 |
| 77 | 21.9 (SD=5.0) | — | 21.1 (SD=5.5) | P > .01 |

TABLE XIII

Degrees centigrade difference between frog cloacal temperatures and air or water.

Rana aurora   Rana pretiosa

Cloacal 1.4 C more than air   Cloacal 1.6 C more than air

Range: -2.9 to 4.6   Range: -1.0 to 5.5

Cloacal 0.1 C more than water   Cloacal 0.8 C more than water

Range: -4.5 to 2.2   Range: -2.2 to 6.0

usually the same as the air, or lower, if the vegetation was wet. The greatest divergence in frog and environmental temperautes resulted if the frog was in direct sunshine and motionless. This basking behavior allows much heat to be absorbed by the frog. Occasionally, a frog caught in water has a temperature lower than the water. This happened when the frog submerged as I caught it. The water below the surface was invariably cooler than that at the surface. I only recorded the warmer surface water in comparing frog and water temperatures.

R. pretiosa used both air and water to raise its body temperature above its surroundings. R. aurora does not bask in the sun while half submerged in the water as does R. pretiosa. The divergence between R. aurora body temperature and that of the water is minimal.

2) Frog temperature tolerance

Frogs of both species can tolerate temperatures of 27-31 C for at least 3 hours, and they show no adverse effects from exposure to these temperatures. Their ability to survive at higher temperatures is summarized in Table XIV, and presented graphically in Fig. 16. No correlations existed between heat resistance and sex or size of the frog.

The onset of heat stress produced different symptoms in each species. Heat stress in R. aurora drastically increases the frogs' levels of activity and swimming. At temperatures below 31 C, R. aurora is relatively inactive, and only infrequently swims rapidly and for long periods. They normally remain motionless at the bottom or sides of the aquarium. At 31 C, they begin swimming very rapidly through the water and try to emerge

TABLE XIV

Ability of frogs to survive high temperatures.

All frogs survived 180 min at 27-31 C

Rana aurora				Rana pretiosa			
N	°C	Min till paralysis mean (SD)	Min till death mean (SD)	N	°C	Min till paralysis mean (SD)	Min till death mean (SD)
10	32	145.7 (59.0)	151.9 (48.9)	10	32	171.0 (28.5)	171.5 (26.9)
21	33	30.2 (22.2)	49.9 (40.5)	10	33	164.8 (48.1)	165.2 (46.8)
5	34	7.8 (7.6)	16.0 (4.8)	5	34	149.4 (25.5)	157.2 (23.8)
–	–	–	–	5	35	77.6 (64.6)	83.6 (27.5)

Figure 16

Temperature tolerance of juvenile and adult <u>Rana</u> <u>aurora</u> and <u>Rana</u> <u>pretiosa</u>.
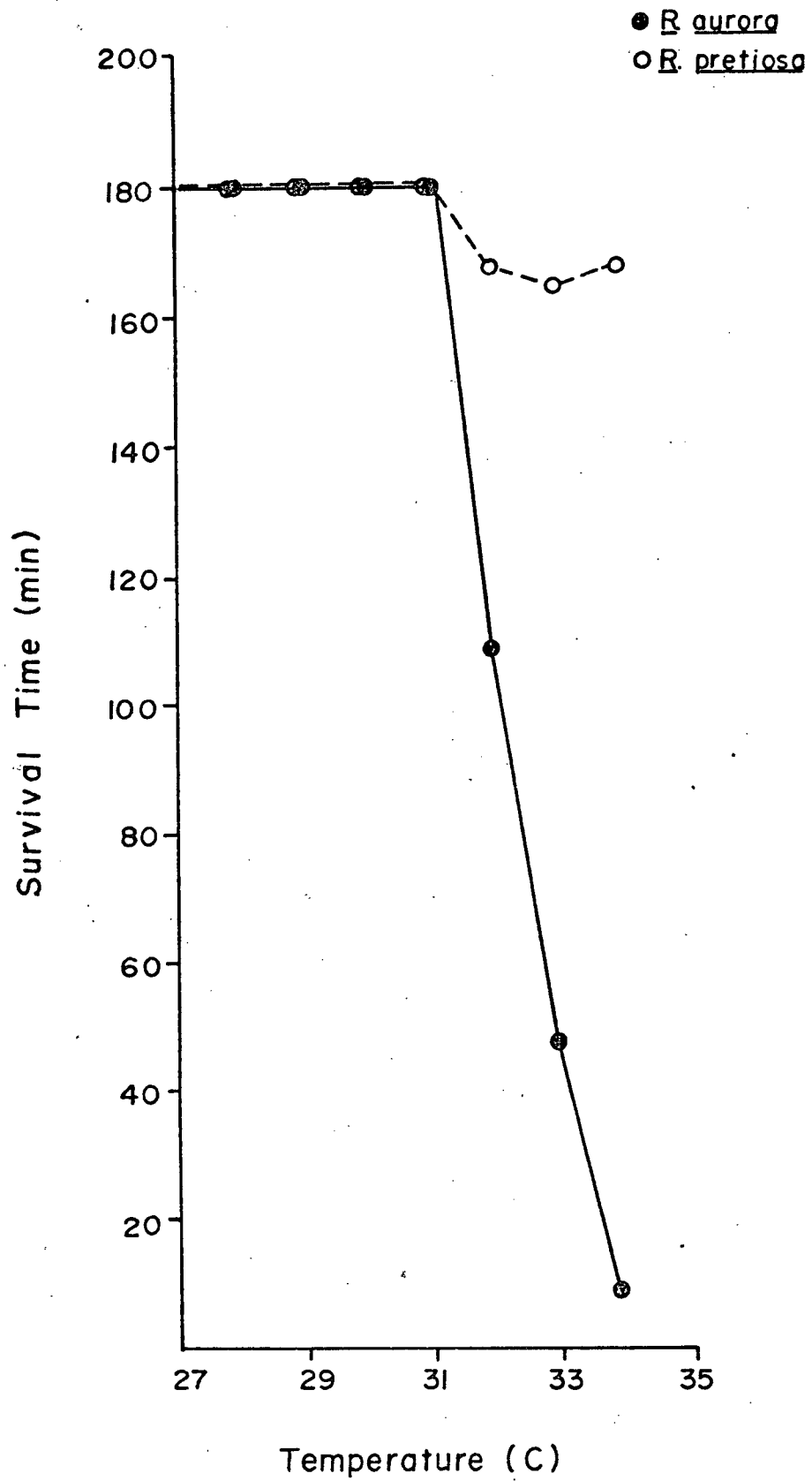
by pushing their heads out. No frogs died at 31 C, but through-
out the 3 hours they were in constant motion. At tests with
higher temperatures, after 31 C was reached, the R. aurora became
hyperactive as before, and then, after varying intervals of time
at the higher temperatures (see Table XIV), paralysis of the
limbs set it. Paralysis of hind limbs is first, and after a
brief period their forelimbs become functionless. Soon the frog
is unable to move its back or head, and sinks to the bottom of
the aquarium. After a few minutes they died. Death is sometimes
preceded by a series of muscular spasms.

Fewer than 50% of R. aurora died at 32 C, but 100% died
at 33 C. The upper tolerance limit for R. aurora is between
32-33 C. Paralysis and death occur rapidly above 33 C.

R. pretiosa is able to tolerate higher temperatures
than R. aurora. The behavior of R. pretiosa is not obviously
affected at temperatures below 33 C. The frogs are not excess-
ively active at 31 or 32 C, but by 33 C, they begin more active
swimming and make frequent attempts to leave the water.

In R. pretiosa heat stress before death is not like
that of R. aurora. The limbs of R. pretiosa keep moving and
paralysis is not marked even above 33 C. Instead, the frogs
become uncoordinated in overall swimming motions, and swimming
becomes slow and difficult. They begin rolling onto their sides
as they swim, and soon swimming becomes slower and is attempted
at only irregular intervals. After final attempts to swim, a
series of spasms from back to head ends in their death. At this
point they sink in the water. As seen in Table XIV the upper
lethal limit for R. pretiosa is between 34-35 C.

d. Water Balance

1) Dehydration

The rate of water loss by evaporation to still air is
a function of the initial body size of a frog; large frogs lose
water at a slower rate than do small individuals. The rate of
water loss reflects, in part, the surface to volume ratio of the
animal being desiccated (Spight 1968).

The results of dehydration tests with frogs at 15 C and
60% humidity are seen in Tables XV and XVI. As expected, small
frogs lose water more rapidly than do larger ones. The relation-
ship between the body weight and rate of water loss is expressed
by the least squares regressions plotted in Fig. 17. R. aurora
and R. pretiosa do not differ in the rate of evaporative water
loss to still air of 15 C (F = 3.40, P > .05).

At 15 C, several small individuals of each species
were exposed to drying conditions until they succumbed from
desiccation. At the point when they were no longer able to right
themselves if turned on their backs (critical activity point -
CAP), they were sacrificed and weighed again. The percentage
weight loss of six small R. aurora at CAP was 34.1% (range 32.3-
37.0%). For six small R. pretiosa, the percentage weight lost
at CAP was 33.2% (range 31.8-34.8). It took from 9-12 hours for
all frogs to die of water loss.

The results of tests at 28 and 25% humidity are
summarized in Tables XVII and XVIII. As was found at the lower
temperature, frogs lose water as a function of their initial
body weight, and this relationship is seen graphically in Fig. 18.

TABLE XV

Rate of evaporative water loss of Rana aurora and Rana pretiosa at 15 C and 60% humidity.

Rana aurora

Body weight of frog (g)	g water loss/hr mean (SD)	g water loss/ g body weight/hr mean (SD)
.98	.048 (.027)	.054 (.030)
1.27	.040 (.022)	.034 (.019)
1.41	.043 (.015)	.033 (.012)
1.68	.062 (.035)	.041 (.026)
1.76	.052 (.020)	.031 (.014)
1.78	.053 (.015)	.032 (.008)
21.75	.212 (.041)	.010 (.002)
22.48	.241 (.029)	.012 (.003)
24.14	.318 (.037)	.013 (.002)
27.22	.277 (.036)	.010 (.001)
28.27	.345 (.027)	.013 (.001)
34.29	.312 (.063)	.009 (.002)

Rana pretiosa

Body weight of frog (g)	g water loss/hr mean (SD)	g water loss/ g body weight/hr mean (SD)
2.63	.060 (.027)	.024 (.009)
2.74	.058 (.029)	.022 (.010)
2.81	.104 (.033)	.040 (.011)
3.01	.075 (.023)	.028 (.007)
3.07	.067 (.031)	.023 (.010)
3.11	.070 (.019)	.025 (.006)
18.29	.207 (.056)	.012 (.003)
22.00	.188 (.050)	.009 (.002)
22.73	.237 (.039)	.011 (.002)
24.87	.285 (.021)	.012 (.001)
27.20	.233 (.036)	.009 (.001)
31.80	.258 (.040)	.008 (.001)

TABLE XVI

Time till Critical Activity Point (CAP) and percentage weight
loss at CAP for small Rana aurora and Rana pretiosa at 15 C
and 60% humidity.

Rana aurora

Body weight (g)	Min till CAP	Percentage body weight loss at CAP
0.98	564	32.7
1.27	552	32.3
1.41	578	34.7
1.68	663	35.1
1.76	635	32.9
1.78	615	37.0
	Mean =	34.1

Rana pretiosa

2.63	672	34.6
2.74	688	32.8
3.01	915	34.8
3.05	750	34.1
3.07	650	31.5
3.11	962	31.8
	Mean =	33.2

Figure 17

Rate of water loss to air of 15 C and 60% humidity as a function of body weight. Lines fitted to least squares regression where y = log rate of loss (g/hr) and x = log body weight (g). For Rana aurora, y = -1.435 + 0.61x and for Rana pretiosa, y = -1.429 + 0.57x.
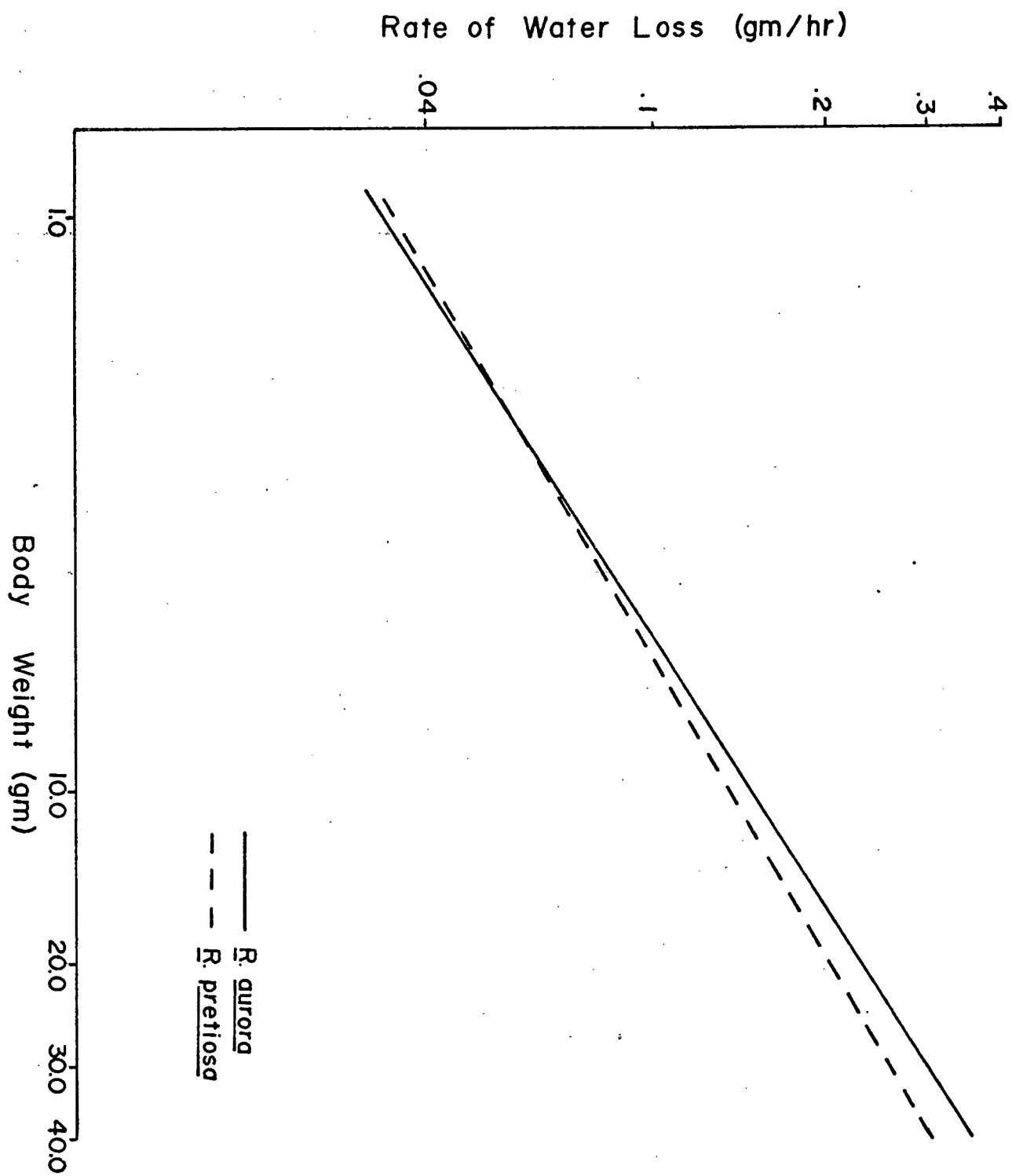
TABLE XVII

Rate of evaporative water loss of <u>Rana aurora</u> and <u>Rana pretiosa</u> at 28 C and 25% humidity.

	Rana aurora	
Body weight of frog (g)	g water loss/hr mean (SD)	g water loss/ g body weight/hr mean (SD)
4.70	.66	.139
5.70	.75	.142
16.95	1.24 (.173)	.092 (.008)
21.41	1.35 (.135)	.075 (.004)
26.37	1.42 (.136)	.060 (.008)
34.02	1.57 (.046)	.051 (.003)
	Rana pretiosa	
7.74	.92	.126
12.46	1.19	.107
15.06	1.27 (.079)	.096 (.014)
16.14	1.27 (.108)	.088 (.013)
16.93	1.22 (.389)	.081 (.017)
21.21	1.55 (.486)	.083 (.016)
28.90	1.83 (.220)	.069 (.004)

TABLE XVIII

Time till Critical Activity Point (CAP) and percentage weight loss at CAP for Rana aurora and Rana pretiosa at 28 C and 25% humidity.

Rana aurora

Body weight (g)	Min till CAP	Percentage body weight loss at CAP
4.70	120	28.1
5.70	140	28.9
16.95	255	32.2
21.41	290	30.7
26.37	345	32.7
34.02	330	25.3
		Mean = 29.7

Rana pretiosa

7.74	170	31.5
12.46	185	28.8
15.06	300	32.7
16.14	310	39.5
16.93	255	32.7
21.21	257	31.4
28.90	345	33.2
		Mean = 32.8

Figure 18

Rate of water loss to air of 28 C and 25% humidity as a function of body weight. Lines fitted to least squares regression where y = log rate of loss (g/hr) and x = log body weight (g). For Rana aurora, y = -.0495 + 0.47x, and for Rana pretiosa, y = -0.498 + 0.51x.
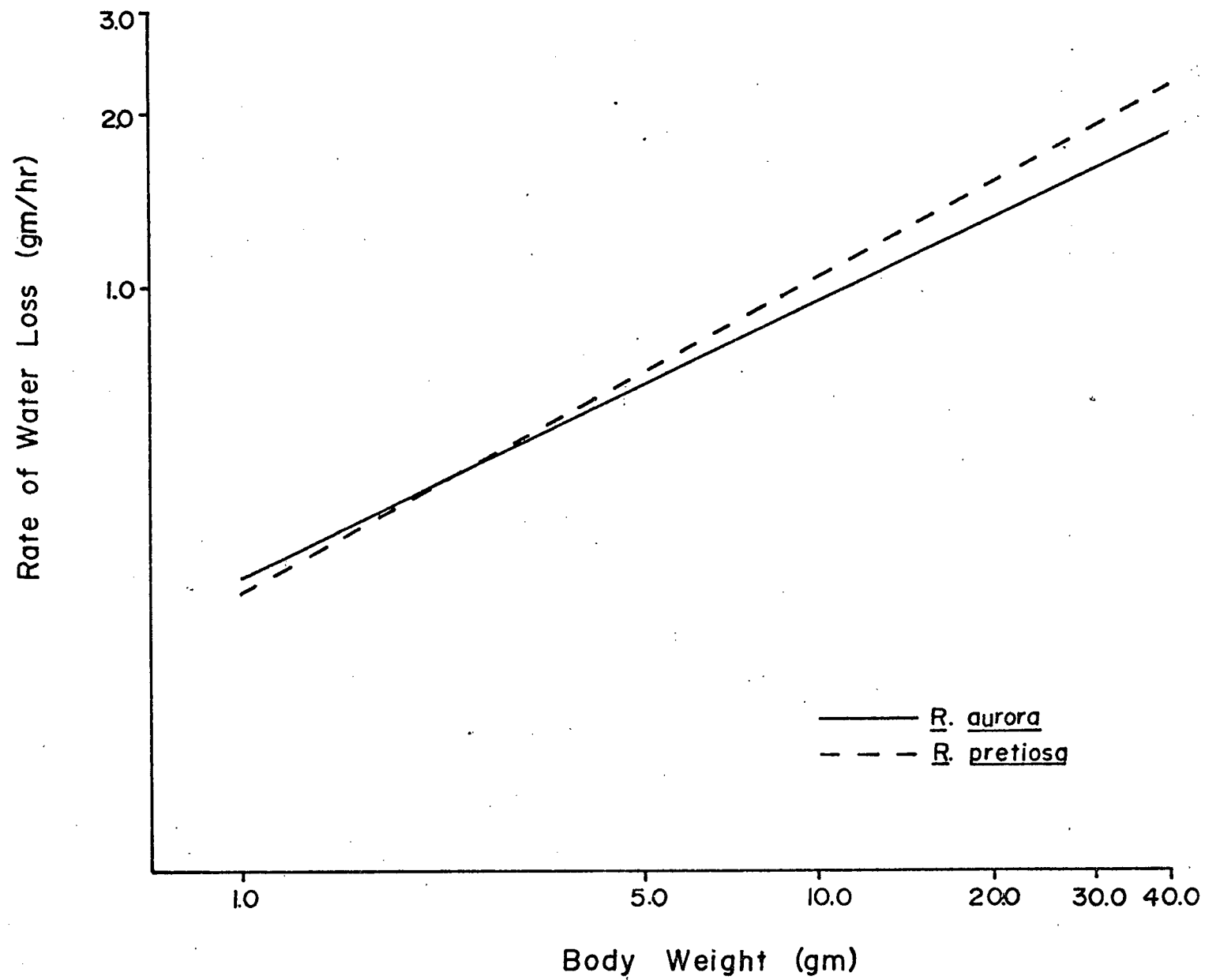
Figure 19

Time till Critical Activity Point (CAP) at 28 C and 25% humidity as a function of body weight.
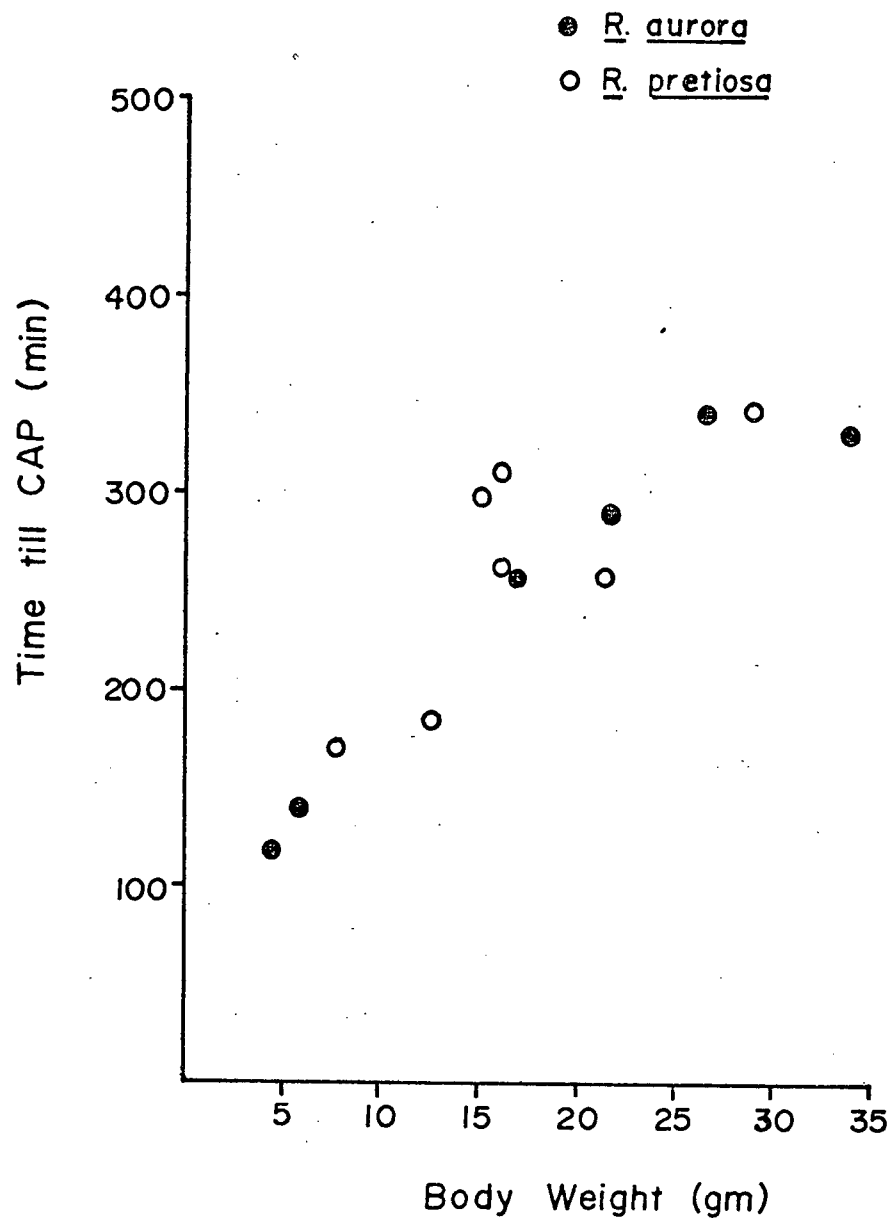
The rate of water loss of the two species does not differ significantly (F = 2.05, P > .05).

At 28 C, all frogs were dehydrated until CAP was reached, and the percentage weight lost at death did not differ significantly between the two species (Table XVIII). The actual time till CAP was reached was also correlated with body size of the frogs. As seen in Fig. 19 large frogs survived longer than small animals, but there appears to be no real difference between the species. There is obvious variability in the time till death. For example, a 34 g R. aurora died sooner than a 26 g R. aurora, and a 28 g R. pretiosa. However, when interspecific comparisons are made, frogs of equal size survived equally long durations.

The total water content of frogs was determined by killing frogs and drying them in an oven for 48 hours at 110 C. Eleven R. aurora averaged 81.3% (SD = .04) of their body weight as water, and eleven R. pretiosa averaged 82.9% (SD = .05). The body water content of intact, healthy frogs of each species does not differ.

The behavior of frogs within the enclosures as they were being dehydrated differed between species, especially at 15 C. From the onset of testing, R. aurora was more active and moved around more than R. pretiosa. Many minutes during each hour of testing, R. aurora tried escaping and crawling within the cages. After these bursts of movement, a frog would settle down, with its limbs tucked beneath its body, in a water-conserving position (Heatwole et al 1969). As an individual R. aurora lost about 20% of its body weight to evaporative water loss, it began showing stress effects and again moving energetic-

ally in presumed escape attempts.

R. pretiosa was less active than R. aurora, and
assumed a water-conserving position almost from the start of
dehydration tests. For several hours, R. pretiosa did not move.
When individuals had lost about 25% of their body weight from
water loss, they became much more active and sought to escape
from the cages. After frantic efforts of several minutes, they
again settled into a less exposed position, that is, with legs
tucked completely beneath their bodies.

2) Submergence tests

Frogs of both species are able to remain completely
submerged in water of 10 C, for eight hours, without showing
adverse effects. The frogs remain completely motionless after
the first hour, and breathing rates are much reduced. When
released from under water and after a few minutes in air, they
are able to move and jump without difficulty.

e. Predator Avoidance

1) Field

In searching for frogs in the LCR study area, I usually
saw R. pretiosa in the river, the pond, or rainpools. From
April to June, rainpools were abundant in the field, and R.
pretiosa was found in or along the margins of the water. As the
rainpools disappeared during the summer, the frogs moved to the
river and stayed there throughout the summer.

The behavior of R. pretiosa, as I approached them, was
to remain motionless, either sitting on the bank, or floating in
the water within the river. If I moved slowly, I could approach

them within a foot or less, but as I reached for them they would rapidly submerge into the bottom of the river, or rainpool, and disappear into the mud. They remained submerged for many minutes (the maximum recorded was 17 in water of 18 C). They then slowly swim to the surface and reappear exposing only their heads or eyes, usually from beneath cover of aquatic vegetation. Any sudden movement causes them to immediately submerge again.

During rains in the summer, R. pretiosa leaves the river and wanders onto land, at times many feet from the river and into the vegetation. When I approached these frogs on land, they immediately hopped toward the nearest body of water (in summer the river). They did not hesitate, but began jumping towards the river. No frog ever hopped away from the river on these occasions. When at the river they immediately submerged into the mud below.

During all months, from April to October, almost without exception, I encountered R. aurora on land moving among the plant cover. Often they were near rainpools, or near the river in summer, but during rain, they move some distance away from standing water. As I approached these frogs, they hopped quickly in the opposite direction, with strong, lengthy jumps. Many times they sought cover in the thick sedges or bulrushes that were widespread throughout the field. After several long jumps, they frequently stopped and remained motionless beneath cover. When near water and frightened, they jump towards water but do not always enter and often seek cover in the vegetation along the bank. If they enter water, they rarely submerge, but swim quickly on the water surface, staying close to the bank and

plant cover along it. They do not readily submerge, but often swim up or down the river and again seek escape on land.

2) Escape behavior after release

Throughout the study I released R. pretiosa along the river bank and scored their escape behavior 194 times. The same was done 121 times for R. aurora. Their escape responses are seen in Table XIX.

Immediately upon release, most R. pretiosa jumped into the river and immediately submerged. Only eleven individuals remained on the water surface, partially hidden by cover. Those frogs that jumped towards land exhibit peculiar jumping behavior. Their jumps became erratic and took a circular course. They jumped very low to the ground, at an angle of about 20°, with a few jumps in one direction and immediately began circling. After five to eight jumps, they had travelled in a small circle and reached the point where they had been released. They did not jump in a straight direction more than two or three times. Some frogs continued making these circular routes three or four times, until they finally found the water and entered it and submerged. Some individuals never found the water and instead, tried to bury beneath the cover of plants on the mud. They hesitated to hop after three or four circles, and indeed, seemed to grow clumsy and trip on their feet. They were easily captured and did not seek further escape.

Most of the R. aurora released on land parallel to the river tried to escape on land (Table XIX). They jumped in a straight direction, at an angle of 45° or more off the ground

TABLE XIX

Escape responses of _Rana_ _aurora_ and _Rana_ _pretiosa_ released
parallel to river bank.

	Rana aurora			Rana pretiosa		
	to water		to land		to water	to land
	42		79		163	31
submerged	remained on surface			submerged	remained on surface	
9	33			152	11	

and went a good distance with each jump. They often sought cover in the vegetation after five to eight quick hops away from the river, or along the bank. ·Those frogs that entered the water stayed on the surface (except for 9 of the 42 individuals) and swam rapidly away along the banks. After swimming several feet, they often turned and faced me, keeping themselves partially concealed by vegetation. After a while some individuals again moved to land and remained motionless on the bank.

3) Jumping ability

The comparative jumping ability of frogs is seen in Fig. 20. The distance jumped is a function in part, of the sv length of the frogs, with bigger frogs able to jump farther. However, as seen in Fig. 20, R. aurora jump farther than R. pretiosa of equal body length. As pointed out in Fig. 10, R. aurora have longer hind limbs than do R. pretiosa, and as Rand (1956) has noted, anurans with long limbs jump farther than those with shorter limbs. The distance jumped by R. aurora and R. pretiosa as a function of their hind limb lengths is seen in Fig. 21, and as expected, R. aurora jumps farther.

The jumping behavior of the two species differs in a way not indicated by distance alone. R. aurora jumps at an angle of about 45°, and R. pretiosa jumps at an angle of about 20°. R. aurora makes three to six jumps in rapid succession, in nearly a straight path. R. pretiosa hops rapidly in small jumps, usually in a circular direction, so that it ends where it had started. They rarely hop in the same direction more than two to four times, but tend to move in a circular direction.

Figure 20

Jumping distance as a function of frog snout-vent length. Lines fitted to least squares regression where y = distance jumped (cm) and x = snout-vent length (mm). For _Rana aurora_, y = 2.56 + 0.70x, and for _Rana pretiosa_, y = 8.95 + 0.25x.
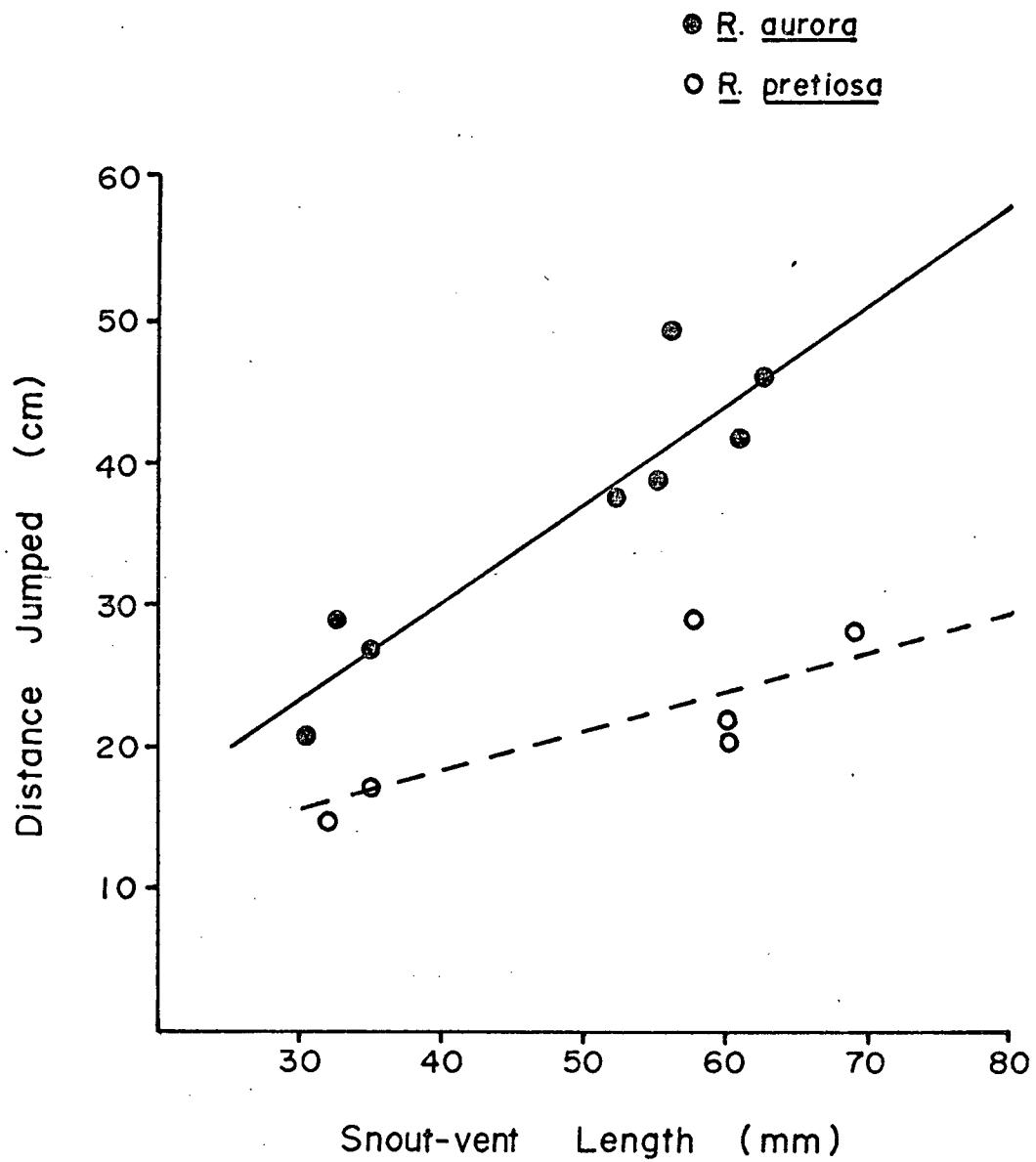
Figure 21

Jumping distance as a function of hind limb length. Lines fitted to least squares regression where y = distance jumped (cm) and x = hind limb length (mm). For Rana aurora, y = 8.79 + 0.31x, and for Rana pretiosa, y = 10.1 + 0.14x.
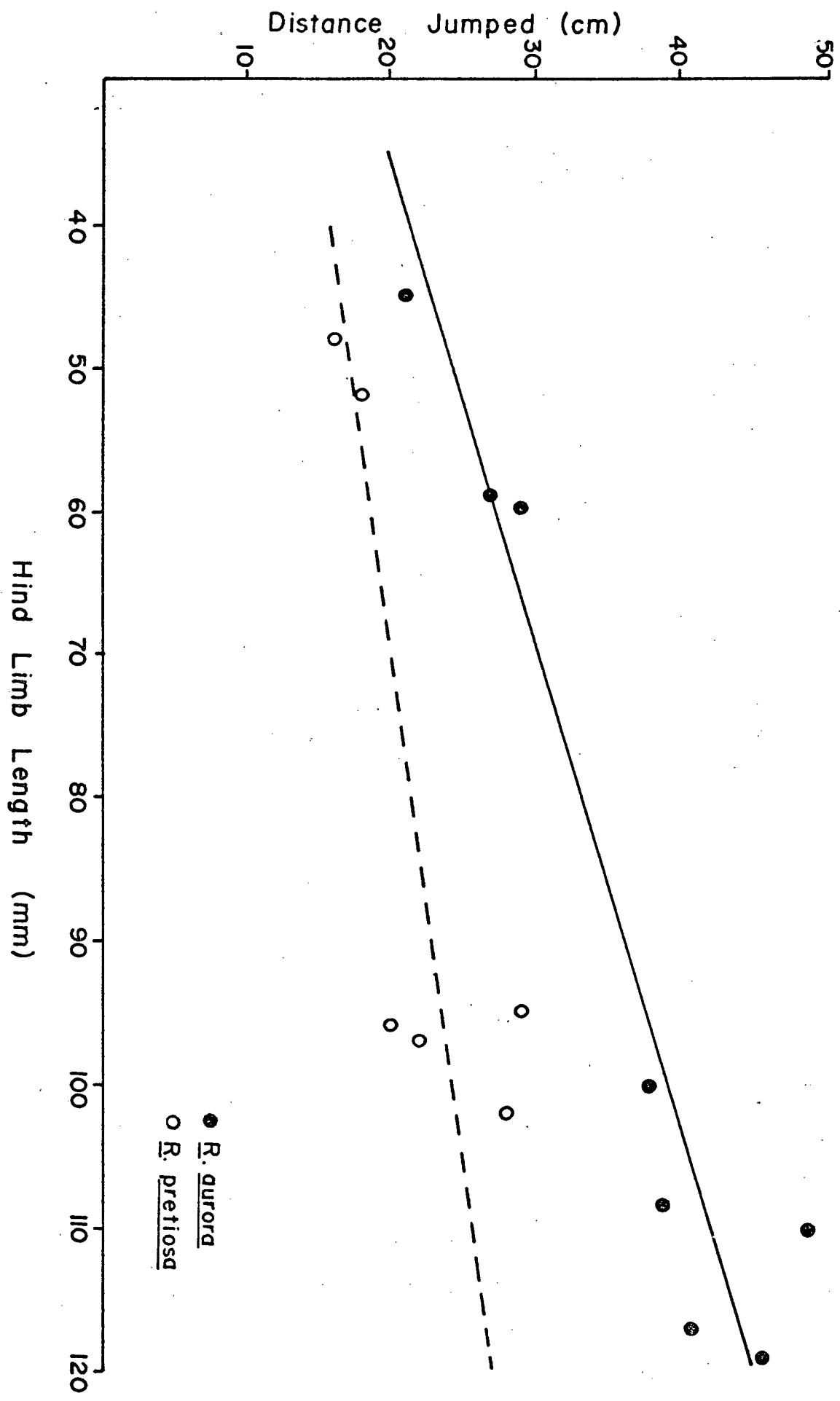
4) <u>Laboratory tests with snakes</u>

The innate escape behavior of laboratory-reared newly metamorphosed frogs was studied by exposing them to their natural predator, the garter snake, <u>Thamnophis</u> <u>sirtalis</u>.

To seek escape from a hunting snake, the frogs could use the moat filled with water purslane, or remain on the mud of the plastic swimming pool used as the testing arena. While the snake was searching for, or chasing frogs, I noted the position of the frogs every 20 minutes. I recorded whether the frogs were on land or in the water. In a series of ten trials lasting two hours each, the position of the frogs was recorded 60 times (three times per hour for 20 hours). <u>R</u>. <u>aurora</u> was on land 50 times and in the water 10 times; <u>R</u>. <u>pretiosa</u> was on land 6 times and in the water 54 times. Each species obviously used a different habitat to escape from the hunting snake. However, the control in this experiment is the behavior of the frogs without a snake present. These results were described in the section on habitat preference and showed that, even without snakes, <u>R</u>. <u>aurora</u> chooses land and <u>R</u>. <u>pretiosa</u> uses water.

The object of these tests was to learn about the general escape patterns of the frogs when confronted with a natural predator. Almost 30 hours were spent watching the frogs' behavior when confined with a hungry, hunting snake. Rather than attempt to quantify their movements, I believe it is sufficient to describe their general patterns of escape responses and means of concealment. Differences were apparent between the species.

A note about the hunting behavior of the snakes is

helpful. A snake gave chase and seemed to be directly aware of the frogs only when they moved. If a frog did not move, the snake would pass within inches and not strike at it. Only when a frog moved did a snake become overtly excited. The smell of the frogs produced searching behavior in the hungry snakes, as judged by the excessive tongue flicking of the snakes in the testing arena, but smell alone, without movements by the frogs did not cause the snakes to pursue the frogs.

R. aurora relied alomst entirely on its jumping ability to escape. Individual R. aurora remained flattened on the ground and motionless whenever the snake approached even as close as two inches. If the snake moved closer, the frog quickly jumped, in relatively long leaps, to the opposite side of the arena. The snake was usually surprised by the jumping frog, but often gave chase several seconds later. The frog had usually jumped fast enough so that it was again able to flatten out on the ground at the far end of the arena, several feet from the snake. If an R. aurora jumped into the moat while fleeing, it quickly left the water if the snake began searching for it there. It sometimes clung to the sides of the moat and slowly crawled out on to the land during the time the snake was searching in the water. Most R. aurora were caught because they jumped from one end of the tank and then back again to where the snake was. However, this is an artifact of the small size of the testing arena rather than inefficient escape behavior under natural circumstances. When caught, almost all R. aurora emitted distress calls, vocalizations like screams, with their mouth wide open (Bogart 1960).

As indicated by the positions recorded for R. pretiosa
as they attempted to escape, this species almost always sought
refuge in the water. Shortly after their initial introduction
into the testing arena, R. pretiosa entered the moat and stayed
there. When a snake began searching the moat, the frog sub-
merged to the bottom, or remained half concealed with the thick-
ness of the water purslane in the moat, showing only its eyes
above the water. Only rarely did R. pretiosa leave the water
and seek escape on land.

When on land, R. pretiosa remained flattened complete-
ly against the mud of the arena. Even when a snake approached
within an inch, the frog did not jump. It did so only when the
snake crawled over the frog or nudged it with its snout. The
frog then began jumping in small, erratic leaps, often in a
circular direction. It was easily caught by a pursuing snake,
unless it found the moat. Of seven R. pretiosa eaten by snakes,
five were caught on land and two in water. Three of the five
had not yet found the moat, but had remained on land since their
introduction into the testing arena. Only one individual gave
a distress call when caught by the snake.

For both species, the main tactic to avoid detection
was to flatten onto the mud when on land. They both stayed
motionless for an hour or more if they were not detected or
disturbed by the moving snake. In water, R. pretiosa relied
on submergence and concealment in the vegetation and R. aurora
used rapid swimming to escape the pursuing snake, until it
could hide.

5) Anuran predators in the LCR study area

In the LCR study area, there occur numerous vertebrate and invertebrate predators of anuran tadpoles and frogs. The following vertebrates were actually seen in the field or are known to occur in the Lower Fraser Valley.

Raccoon (*Procyon lotor*). Raccoons were never seen feeding in the field, but their tracks were numerous all along the course of the river. During all seasons of the year, new tracks were seen, indicating raccoons fed along the river in the field.

Great blue heron (*Ardea herodias*). On virtually every visit to the field in spring and summer, I saw either one or two herons feeding in or along the river in the field. Herons were usually seen in precisely those places where newly metamorphosed frogs were most abundant. I saw a heron catch two adult R. pretiosa, but I was never able to identify other prey. Frogs were certainly a major part of their diet, as they are in other parts of the Lower Fraser Valley (D. Short, per. comm.).

Belted kingfisher (*Megaceryle alcyon*). During the spring and summer when tadpoles are still in the river, on numerous visits I saw kingfishers diving into the river.

Garter snake (*Thamnophis sirtalis*). This snake is a major frog predator throughout its range. It is very abundant in the LCR study area, and I caught 30 different individuals (none were removed). When made to regurgitate their food, eight snakes had remains of frogs or tadpoles. One snake was caught eating a newly metamorphosed marked R. aurora, and another just eating a 47 mm male R. pretiosa. Many snakes escaped capture, and

almost all were seen along the pond and river where tadpoles and frogs live.

Northwestern salamander (Ambystoma gracile) and Rough skinned newt (Taricha granulosa). The larvae of the urodeles are voracious tadpole predators, and the neotenic form of A. gracile also eats tadpoles. The larvae and neotenic adults of A. gracile are very numerous in the river. They will consume hundreds of tadpoles in a week as I observed in the laboratory.

The above vertebrates are probably major predators living in the LCR study area. They normally eat anurans and are very abundant. The following predators may add to the general predation pressure on R. aurora and R. pretiosa: cutthroat trout (Salmo clarkii), red-tailed hawk (Buteo jamaicensis), marsh hawk (Circus cyaneus), great horned owl (Bubo birginianus), red fox (Vulpes fulva), striped skunk (Mephitus mephitus), mink (Mustela vison), feral housecat (Felis domesticus).

A wide variety of invertebrates found in the LCR area prey especially on tadpoles. However, the giant water bug (Lethocerus americanus) is capable of eating small frogs. In June 1968, I caught 83 Lethocerus nymphs and adults from the pond. In the river they are very numerous and are probably a threat to small R. pretiosa.

The leech (Batrachobdella picta) is extremely abundant in the pond and river. They were found attached to about 75% of all R. pretiosa captured, and in June some frogs had as many as 20 small leeches attached. They occur on R. aurora to a much lesser extent, because of R. aurora's preference for land as a habitat.

TABLE XX

Summary of differences in morphology, ecology, and behavior
between <u>Rana</u> <u>aurora</u> and <u>Rana</u> <u>pretiosa</u>.

<u>Rana</u> <u>aurora</u> - terrestrial	<u>Rana</u> <u>pretiosa</u> - aquatic
Morphology	Morphology
longer legs	shorter legs
eyes lateral	eyes dorsal
little mucous	copious mucous
bold pattern	more uniform in color
Ecology	Ecology
actively searches for food	waits to ambush prey
feeds on land	feeds from water
upper thermal tolerance 33 C	tolerates 35 C
Behavior	Behavior
jumping good	jumping poor
long straight jumps	circular jumps
uses land to escape from predators	uses water to escape from predators
in water, clings to vegetation and swims on surface in escape behavior	in water, submerges to bottom to escape

A summary of the main differences in the morphology, ecology and behavior between R. aurora and R. pretiosa is seen in Table XX.

C. Comparative Reproductive Behavior

a. Prebreeding and Breeding Behavior of Rana aurora

1) Emergence from hibernation and migration to breeding sites

The first R. aurora appear as soon as ice and snow begin melting from the river and field. Frogs have been found overwintering in both river and woods, and the duration of ice cover primarily affects the time of emergence. In 1968, the last ice melted about 14 February, and daily searches were first successful on 24 February when several males were caught. In 1969, frogs were first caught on 3 March, the unusually pro-longed ice and cold having delayed emergence. The temperature data for both years (Fig. 22) indicate that R. aurora first become active when the air has been at least 5 C for several days. If temperatures fall below this after emergence, the frogs apparently become inactive. (Subadult frogs did not appear for the first time until several weeks after breeding terminated, and air temperatures were daily above 10 C.

Very soon after emergence, R. aurora begins to move to breeding sites. Most movements occur at night and seem to be stimulated by cloud and precipitation, conditions under which higher temperatures prevail. On clear days, some frogs were caught active during daylight hours, but most were found during dusk, before the rapid drop in temperature accompanying the

Figure 22

Air and water temperatures and precipitation data for 1968 and 1969, pertinent to the breeding behavior of _Rana aurora_ and _Rana pretiosa_ at the Little Campbell River study area. Single arrows indicate dates on which _Rana aurora_ males began calling; double arrows indicate the same for _Rana pretiosa_ males.

1968

Daily Precipitation

2"
1"
0"

Daily Max Air Temp (C)

12
8
4
0
-4

Daily Min Air Temp (C)

12
8
4
0
-4

Daily Max Water Temp (C)

Daily Min Water Temp (C)

5 10 15 20 25 1 6 11 16 21 26

February   March

1969

Daily Precipitation

2"
1"
0"

Daily Max Air Temp (C)

12
8
4
0
-4

Daily Min Air Temp (C)

12
8
4
0
-4

Daily Max Water Temp (C)

Daily Min Water Temp (C)

25 2 7 12 17 22 27 1 6 11
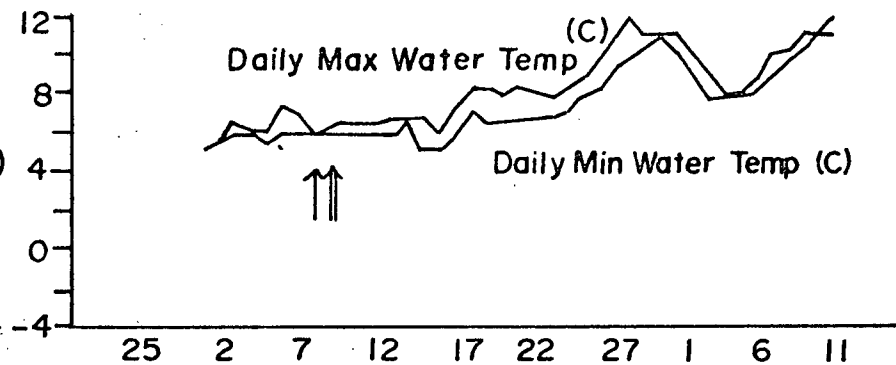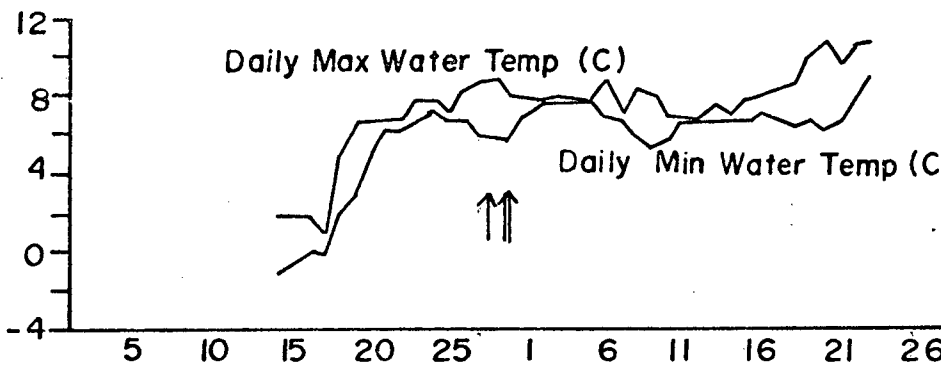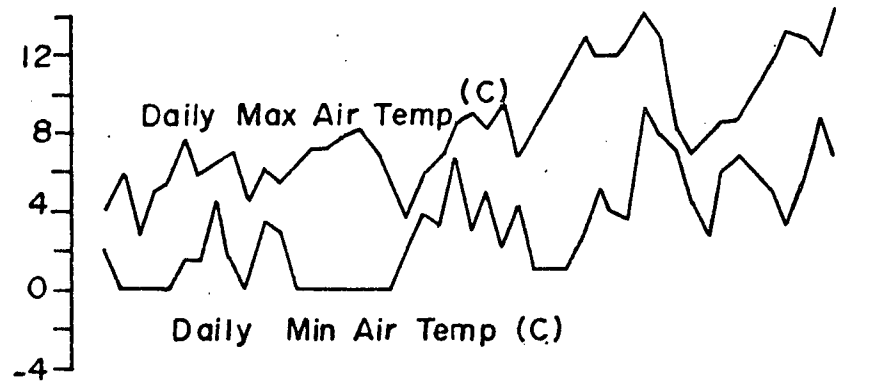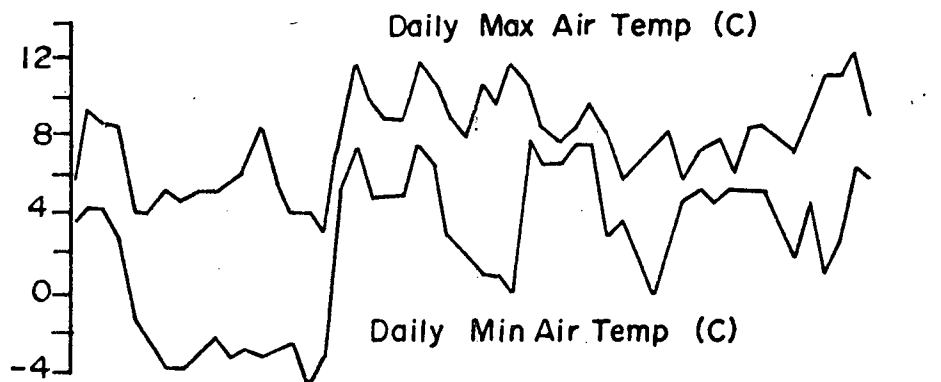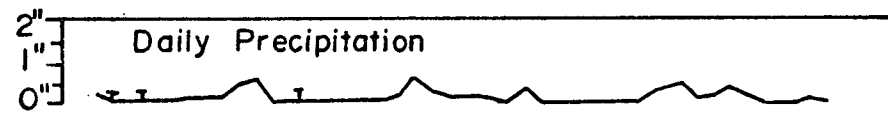
February   March   April

onset of darkness. In both years, by about one week after emergence, several dozen males had arrived at the breeding sites.

The breeding sites were in the northern ends of the pond and adjacent portions of the river.

2) Prespawning activity at breeding sites

Males arrived first at the pond and river breeding sites and remained concealed, often in full sunlight, near sedges and bulrushes. No feeding activity was noticed at this time, and the frogs quickly entered the water when approached. In the first week after emergence, no female R. aurora were found at the breeding sites, but several were found 150-300 ft away in the field.

Males were at the breeding sites at least one week before they began to vocalize. Not a single call was heard in a full week of almost round-the-clock observations, yet more males were found at each search. This suggests that the males find these sites and orient to them without use of vocal cues from other males already at the sites.

Although the males are not vocal when first gathered at the sites, experiments show that they will persistently and tenaciously clasp a female R. aurora, or any other animal of suitable size, if given a chance. Male R. aurora, collected from breeding sites before calling had started and placed with female R. aurora (or R. pretiosa) in aquaria, quickly assumed amplexus. At Stanley Park, about 1900 hr on 19 February 1968, a pair of R. aurora was caught in amplexus, and on 20 February, about 2000 hr in Stanley Park, a male R. aurora was seen tightly

clasped with a male salamander, <u>Ambystoma</u> <u>gracile</u>, which finally broke free after a 10-minute struggle. Thus calling and initiation of a chorus is not a necessary prerequisite for sexual arousal in male <u>R</u>. <u>aurora</u>.

3) Vocalizations at breeding sites

Male <u>R</u>. <u>aurora</u> began calling after about one week at the breeding sites. In 1968, after several days of listening with no indication of vocal activity, I first heard the calls on the afternoon of 28 February, and in 1969, on the afternoon of 8 March. Stimuli responsible for initiating the calling are uncertain, but rising temperatures seem especially important. In both years, the water and air temperatures were above 6 C for several days before calling started. Temperatures in the pond where frogs had gathered had not fallen below 6 C for five to seven days before initial vocal activity (Fig. 22).

Unpaired male <u>R</u>. <u>aurora</u>, at every breeding site observed, emit their mating call while completely submerged under water seven inches to three ft in depth (up to 15 ft in Marion Lake). They normally remain stationary on the bottom or concealed in tufts of submerged vegetation. Of numerous males observed in daily and nightly recording sessions, only two were observed to call above water, which they did only briefly before submerging again. Males call several feet apart and remain motionless on the substrate or in vegetation. At indefinite intervals they surface for air, and may swim a few inches above water, usually returning and submerging very near the spot from which they surfaced.

The mating call of R. aurora is very low in volume and has little carrying power. The calls, given underwater, as they normally are, are barely audible in air; if the frog is calling in several feet of water, no sound at all can be detected in air, and a hydrophone is necessary to detect the calls. Frogs calling near the surface in shallow water produce calls heard, at most, 20-30 ft away in air. Mating calls given above the water cannot be heard beyond 50 ft. Males calling in about two feet of water at 12.8 C emit calls which carry about 30 ft underwater, as verified by use of a hydrophone.

The intensity of calls given above water by a male two feet away from the sound meter reached a maximum of only 3 db. The call is less intense if given underwater and measured directly above the calling male at the water surface.

The calls have a definite ventriloquial effect and first appear to emanate from frogs vocalizing some distance away. They are almost completely masked by the loud "chorus" of the Pacific treefrog (Hyla regilla, which often calls simultaneously. (For comparison, note that a single Hyla calling 15 ft away from the sound meter gives calls having a maximum intensity of 10 db.)

Observations at Marion Lake emphasize the unusual behavior of calling male R. aurora. On 8 April 1969, at 2100 hr, I listened in air for sounds of male R. aurora I knew to be present in the lake. Not a single call was heard from any position around the lake or from a boat in the center of the lake. However, on listening beneath the water with a hydrophone, I heard the mating calls of several hundred R. aurora. The

entire lake, beneath the water, resounded with the calls of frogs submerged at depths up to 15 ft. The same series of events was repeated the next day.

At the LCR study area, R. aurora males were found to call during the day, but most were vocal during the night and early morning. When calling has begun for a season, it may continue nightly until breeding has terminated. Low air temperatures at night do not seem to affect the males calling submerged in the warmer water.

Mating calls are emitted at indefinite intervals, but there seem to be cycles of maximum intensity in a "chorus" throughout the night. Males call more frequently when other males move near them. When two males approach, they rapidly repeat their mating calls in quick succession, doing so until they attempt mutual amplexus, emit release calls, and swim away. Any movement near a calling male stimulates him to call more often, at times up to 30 seconds without cessation.

The mating call of unpaired R. aurora has not been described previously by analysis with the sound spectrograph. The call consists of either two, three, four, or five notes, but almost all calls are three or four notes. A sonagram for a typical mating call given by a male 58 mm (sv length) calling submerged in water 9 C is seen in Fig. 23.

Each individual note consists of five to six separate pulses. There is a rise in pitch and intensity on the last notes within a series. The dominant frequencies of the notes lie between 450 and 1300 Hz, and the notes may extend to 7.5 kHz.

<u>Figure 23a,b</u>

Sonagrams of male <u>Rana</u> <u>aurora</u> vocalizations. a. Mating call of
an unpaired male submerged in water 9 C. b. Single note emitted
once a second by a male clasped with a female.
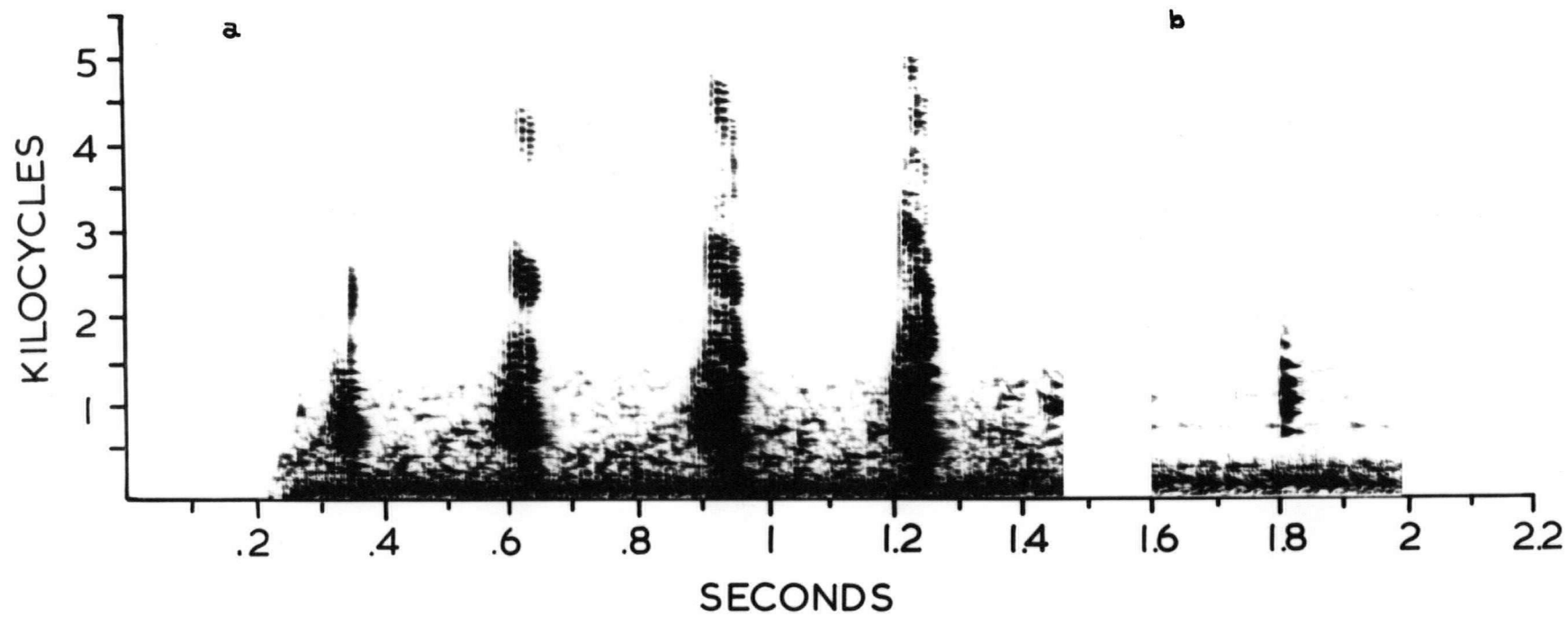
A call with four notes lasts about 1 sec (0.90-1.00 for 12 calls from three males in water at 9 C). A five-note call lasts about 1.25 sec. The call can be compared to a repeating series of the sound 'uh', with more emphasis placed at the end of the series: uh uh uH UH.

4) Behavior of amplectic pairs

Male R. aurora clasp females in an axillary position as described by Storm (1960) and pictured in Licht (1969a), and as seen in other ranids. The male holds very tightly and it requires some effort to remove him from a female. While clasping, the male emits a single call note, about once every second. As the male gives this note, his throat pulses and his abdomen contracts, causing him to pull slightly backwards as he grips the female. He makes this sound with his mouth directly behind the female's tympanum.

This single note is very constant in structure and is essentially a burst of energy between 750 and 1500 Hz (Fig. 23). The spectral characteristics of the note fall within the range of dominant frequencies of the mating call. The note is unpulsed and lasts only .05 seconds. It is extremely low in volume and cannot be heard beyond one to two feet from the amplectic male in a quiet room. It is at most 1 dB in intensity when measured six inches away. However, this note is emitted directly into the female's ear and consequently may be more intense for her.

Males clasped with receptive females emitted this sound continually. Without cessation, a male continually repeated this note almost every second for a full hour during which

he was observed. It is given both underwater and in air, if the amplectic pair is placed out of water. Males also give this call when clasped with females which are unreceptive and attempting to gain their release, but when the female becomes very active, the male ceases and emits a different kind of call as described by Licht (1969a). Males from all populations studied gave the single note when clasped, and it seems to be a normal part of their vocal repertoire during breeding.

The second type of call amplectic males emit is a series of one to eight notes which differ in temporal and structural pattern from the mating call of unpaired males (see Figs. 7, 8 in Licht 1969a, and Fig. 23 in this report). This amplectic call has been recorded from males clasped with unreceptive females both in the field and laboratory, but it is not yet certain that this call is given by males clasped with receptive females. However, there is some preliminary evidence that it may. A hydrophone was held near a pair of R. aurora in 2 ft of water at Marion Lake. The male did not give this amplectic call as the female remained still, but as she began to swim a few inches, the male began vocalizing. When she stopped swimming, he stopped calling. On another occasion, in the laboratory, a male R. aurora was clasped with a female R. pretiosa which remained quiet and did not struggle. She was thus a 'simulated' receptive female R. aurora. They were left alone in a darkened room and not disturbed, but recordings were made of all vocalizations. The male spontaneously emitted amplectic calls (series of one to eight) at intervals. Subsequent observations indicated that the male called whenever the female R. pretiosa began to swim.

Sonagraph analyses of male R. aurora release calls
(those calls given by males when they come physically in contact
with other males, and identifying the caller as male) and male
amplectic calls reveal much similarity. The release calls are
highly variable in both spectral and temporal pattern and are
not easily quantified. Males are in varying states of excite-
ment when they emit the release calls, but in general calls are
more intense (more energy) and more rapidly repeated than the
amplectic calls. Although they cannot be considered the same
call types, the amplectic call seems to be a modified version of
the male release call.

A male R. aurora is quickly forced to release an un-
receptive female R. aurora which undergoes elaborate and ex-
tensive behavior to gain her release. When placed in aquaria
with two inches of water, an unreceptive female can secure her
release in less than one minute (Licht 1969a). Further tests
were conducted with unreceptive females placed in tanks contain-
ing water one or two ft deep. Under these circumstances, when
clasped by a persistent male R. aurora, the female attempts to
gain her release by continually rolling over in the water and
issuing release calls. Persistent males will maintain their
grip for as long as 15 minutes, but eventually relax their
clasp on the female. The same females, when placed in only two
inches of water, can gain their release within a minute, owing
to their ability to use the substrate to maneuver more easily.

5) Spawning Behavior

During both years at the LCR, the initiation and
termination of egg laying was precisely determined. Egg laying

started on the night of 28 February and ended on 13 March in 1968, and in 1969, it began on the evening of 15 March and stopped on 3 April. Once egg laying began it was intensive, and most females spawned within two weeks after the first egg was found (Table XXI). Weather data seen in Fig. 22 indicate that water temperature of 7 C is sufficient for spawning and that once this minimum is reached, most eggs are deposited. In 1969, only one egg mass was deposited before the pond reached at least 7 C.

In both seasons, all eggs were deposited overnight as determined by dusk and dawn visits to the LCR site. Although males may vocalize during the daylight hours, the females apparently spawn only during the dark (it is unknown whether they respond to the male call during the night or day).

Egg masses were attached to stalks of submerged vegetation (Typha, Carex, and Potomageton) at minimum depths of 12 inches and as deep as 3 ft (up to 15 ft in Marion Lake). The eggs are placed in quiet water with little or no flow, and in areas exposed to sunlight for most of the day. Masses were usually 2 ft or more apart from each other, but at each distinct site at the LCR, the eggs are laid in the same general vicinity. For example, ten masses were deposited within 20 sq.ft. in the river. The eggs often become covered with a film of debris and may be difficult to distinguish, but if one mass is found, a careful search will reveal others nearby.

In the LCR pond, R. aurora deposits its eggs in the center where water is deepest (2 - 3 ft), and about

TABLE XXI

Numbers of new <u>Rana</u> <u>aurora</u> egg masses found on each search at
the Little Campbell River during the 1968 and 1969 breeding
seasons.

1968		1969	
Date	No. masses	Date	No. masses
February 26	0	March 12	0
27	0	13	0
28	1	14	0
29	5	15	1
March 1	2	16-22	0
2- 5	2	23	3
6	0	24	0
7	4	25	5
8	1	26	3
9	0	27	10
10	8	28-31	0
11	0	April 1	0
12	8	2	0
13	5	3	11
14	0	4	0
15	0	5	0

3-15 ft from the pond edge. In the river, the eggs are laid in water two to four ft deep, close to the main channel at the deepest part of the overflow. No R. aurora mass was found within four ft of the shoreline and submerged less than 18 inches deep. The oviposition sites are those at which males vocalize.

In the LCR locality in 1968, the first R. aurora mating calls were heard on 28 February and the last egg mass laid on 13 March. In 1969, these dates are 8 March and 3 April. Thus the effective breeding season lasted 15 days in 1968 and 27 days in 1969.

b. Prebreeding and Breeding Behavior of R. pretiosa

1) Emergence from hibernation and migration to breeding sites

Emergence from overwintering sites begins as early in the year as the winter thaw permits. Frogs were first caught on 21 February 1968, and 3 March 1969. Air temperatures of 5 C is evidently the minimum necessary for initial activity, but several males seen basking in the sun probably had higher body temperatures.

The males arrive first at breeding sites and on arrival they remain in shallow water at the edges of the pond and along the margins of the river overflow. From 3 to 9 March 1969, about 18 or more males gathered into two separate areas. About eight males were within a 3 ft square area at the edge of the pond where bulrushes provided cover. Ten or more males were within a similar area along the shallows of the river, about 65 ft away from the pond. A few solitary males were caught scattered along the river and pond borders about 10-20 ft from

the main groupings, and they remained apart from the aggregations before calling started. All males were basking in the sun or floating on the water surface.

2) Vocalizations and male behavior at breeding sites

Calling by unpaired males at breeding sites began on 29 February 1968, and on 9 March 1969. The first calls were noted in the afternoon when the air temperatures were about 12 C in direct sunlight at the calling sites. Calling continued throughout the afternoon and into the evening, but ceased on some nights when temperatures were near freezing. Within a day or two after calling began, solitary males initially found away from the main aggregations, and individually marked by toe clipping, were recaptured within the groups of males.

Males called from within one ft of each other, and as many as six may cluster into an area two ft square. They called while floating on the water surface with their heads up, or sitting above the water on mats of vegetation: they were not observed to call underwater. They remained in the shallows of the pond or river overflow in water only two to six inches deep, and virtually all males faced toward shore as they called.

On the first few days after calling began, the males in close proximity constantly clasped each other. Whenever a male moved, it attracted the attention of a nearby male which swam towards it and attempted amplexus. After breaking apart, both males would remain still for many minutes until they would again attempt amplexus or move apart. After several days of this behavior, these bouts of mutual amplexus were no longer

seen, and thereafter the males remained within inches of each other, vocalized, but did not clasp.

The mating call of R. pretiosa males is usually a series of short bass notes from six to nine in number, but notes of four to 26 in a series are also given. About noon, on 26 March 1969, when the water was 13 C, I counted the notes of 163 calls given by seven males. Twenty-seven had six notes, 48 had seven notes, 47 were eight notes, and 23 had nine; the rest were either four, five, ten or twelve notes. However, it was observed that as a male approached another frog, the number of notes increased, and reached as many as 26 before that call ceased. Playback of recorded calls on tape loops to nearby males continually evoked prolonged calls from them.

The call of R. pretiosa is low in volume and carries only 50-100 ft at most. The first two or three notes in a call are barely audible, but the intensity increases with each succeeding one. A male calling four ft away from the sound meter gave mating calls which were 4-5 db. The call of Hyla regilla completely masks the low bass notes of R. pretiosa.

A sonogram of a typical call with ten notes is seen in Fig. 24. Each note is unpulsed and lasts about 0.03 sec. At 11.4 C the interval between notes within a call is 0.11-0.14 sec, and a call of seven notes lasts 1.10-1.22 sec. Each note contains dominant frequencies between 0.5 and 1.5 kHz, and the last notes within a call extend, with reduced energy, to about 5.5 kHz.

Figure 24

The mating call of an unpaired male _Rana_ _pretiosa_ floating in
water 12.4 C.
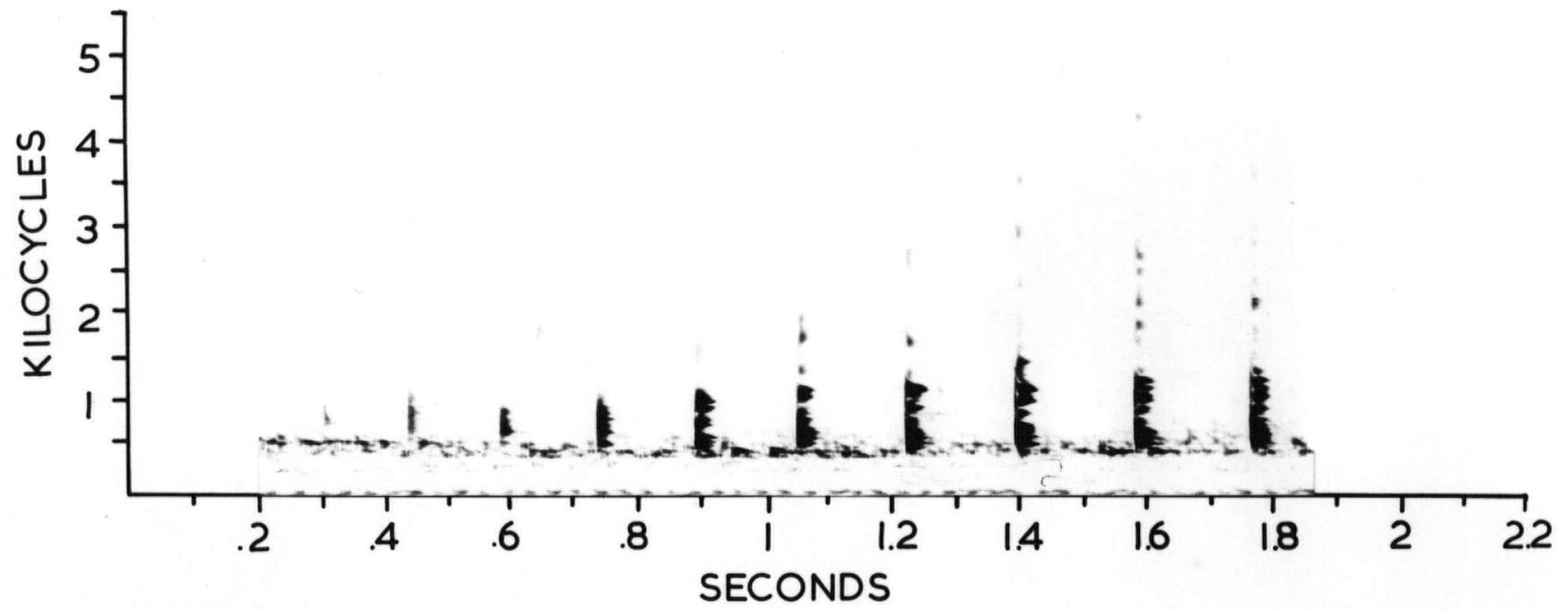
3) Behavior in amplexus and spawning

Before amplexus, females find their way to the breeding sites and there remain within range of the males' mating calls. They remain apart from the males until ready to spawn. For example, in 1969, four females were found about 75 ft from the pond several days before the males began to give mating calls, and three were recaptured in the same area on successive days. One female first caught on 3 March was caught again in amplexus on 12 March, in the pond 60 ft from where she was originally found.

During both years, eight amplectic pairs of R. pretiosa were encountered, and all but one pair were found in bright sunshine in mid-afternoon, with air temperatures about 15-16 C. Pairs remained very still in shallow water only two to five inches in depth, with the male's back often three-quarters out of water. No calls from amplectic male R. pretiosa were detected, although two males gave rapid 'trills' when first grasping a female and assuming amplexus; the clasp is axillary as in other ranids. Unreceptive female R. pretiosa secure their release by use of release calls and abdominal vibrations.

The first egg masses in 1968 were deposited on 1 March, and in 1969 on 13 March. Subsequent egg masses appeared within several days as seen in Table XXII. The eggs were mostly deposited during mid-afternoon, but during the night as well.

In each area where males called, the eggs were deposited in one spot. The masses were usually deposited on top of, or immediately touching, a mass already present. For example, clusters of 26, 19, and 11 masses were found in areas less than

TABLE XXII

Numbers of new _Rana pretiosa_ egg masses found on each search at Little Campbell River during 1968 and 1969 breeding seasons.

1968		1969	
Date	No. masses	Date	No. masses
February 26	0	March 12	0
27	0	13	15
28	0	14	0
29	0	15	0
March 1	3	16	1
2-5	10	17	0
6	0	18	0
7	15	19	9
8	0	20	1
9	0	21	18
10	2	22	0
11	0	23	10
12	0	24	0
13	0	25	0
14	0	26	0

two ft square. The smallest number found together was five. The masses are not attached to any vegetation and are deposited in such shallow water that only the bottom half of each is submerged while the tops are exposed directly to the air.

This clustering phenomenon is directly due to the behavior of both the male and female. On four different days, males were observed calling from the surface of the egg jelly, while other males were calling only inches away. More striking evidence is that females may actually seek out egg masses already present on which to deposit new ones. On 20 March 1969, a female was observed depositing the first eggs in an area where males had been calling for several days.

The next day there were 18 new masses surrounding or touching that one. I moved all 19 masses to an identical spot four ft away. On 23 March, two other masses had been added to the surface of the others and a third mass was deposited only three inches away. No new masses were added to the new or original sites on subsequent days, but these preliminary manipulations suggest that there are in female R. pretiosa specific behavioral adaptations for grouping of egg masses.

Sites used for egg-laying in 1969 were within one ft of those used in 1968. A third new site in the river was also used in 1969. As will be discussed, two sites were within 10 ft of those used by R. aurora, although the specific area chosen differed in several respects.

In 1968, the effective breeding season was 11 days, and 15 days in 1969, as determined by the first day of calling and last day of egg laying.

TABLE XXIII

Summary of main similarities and differences in the prebreeding
and breeding behavior of Rana aurora and Rana pretiosa at the
Little Campbell River study area.

Rana aurora	Rana pretiosa
(1) Emerge from hibernation in February and March	(1) Same
(2) Move to breeding sites when air is minimum of 5-6 C.	(2) Same
(3) Use the northern portions of pond and river for breeding.	(3) Same
(4) Males vocalize several feet apart	(4) Males vocalize inches apart in small groups.
(5) Males vocalize under several feet of water at least 3 ft from shoreline.	(5) Males vocalize in air from shallow margins of pond and river.
(6) Calls given mainly at night but may occur during the day.	(6) Calling occurs during daylight and on nights above 5-6 C.
(7) Females spawn during the night.	(7) Females spawn during the day, often in full sunshine.
(8) Eggs laid several feet apart attached to vegetation in depths of 12 inches or more and 3 ft or more from margins of pond and river.	(8) Eggs laid in groups unattached in only a few inches of water at river and pond margins.
(9) In 1968 calling began 28 February and spawning ended 13 March; 8 March and 3 April in 1969.	(9) Calling began 29 February and spawning ended 10 March in 1968; 9 March and 23 March in 1969.

A summary of the main similarities and differences in the prebreeding and breeding behavior of R. aurora and R. pretiosa is seen in Table XXIII.

D. Embryonic Thermal Requirements and Environmental Temperature

a. Rana aurora

The eggs of R. aurora are loosely enclosed in a compact oval jelly mass attached to vegetation at least 18 inches below the water surface. The eggs are large. The diameter of 186 individual eggs from nine egg masses averaged 3.03 mm (SD = .29).

The percentage survival of stage 20 from stage 4 at different temperatures is shown in Table XXIV. No eggs at 1-3 C survived beyond stage 11. Although mortality is slightly greater than 50% at 4.5 C, this temperature is not believed to be lethal. Eggs that were still alive at stage 18 were attacked by a fungus, and apparently died as a result of this infection. (Embryos were seen moving within the fungus-coated jelly capsules, but were dead by stage 20). Consequently, the lower lethal temperature is probably slightly lower than 4.5 C.

Between 4.5 C and 20 C, development proceeds normally, and these temperatures are considered to represent tolerable limits. At 23 C, the embryos underwent abnormal gastrulation (stage 11), and were deformed in successive stages. About 10% of these reached stage 20, but all were badly misshapen and soon died. At 24 C and 25 C, all embryos died shortly after abnormal gastrulation.

The fact that most embryos survived at 20 C whereas at 23 C all failed relatively early (at stage 11), indicates that

TABLE XXIV

Percentage survival of eggs to stage 20 at constant temperatures.

Incubation temperature C	% survival	
	Rana aurora	Rana pretiosa
1 - 3	0	0
4.5 ± .5	47	0
7.0 ± 1.0	84	76
10.8 ± 1.0	93	87
15.0 ± 2.0	90	–
20.0 ± .1	86	86
23.0 ± .1	0	–
24.0 ± .1	0	93
25.0 ± .1	0	–
26.0 ± .1	–	90
28.0 ± .1	–	94

– indicates eggs not tested at that temperature.

Figure 25

Rate of development of eggs of _Rana aurora_ and _Rana pretiosa_.

R. pretiosa
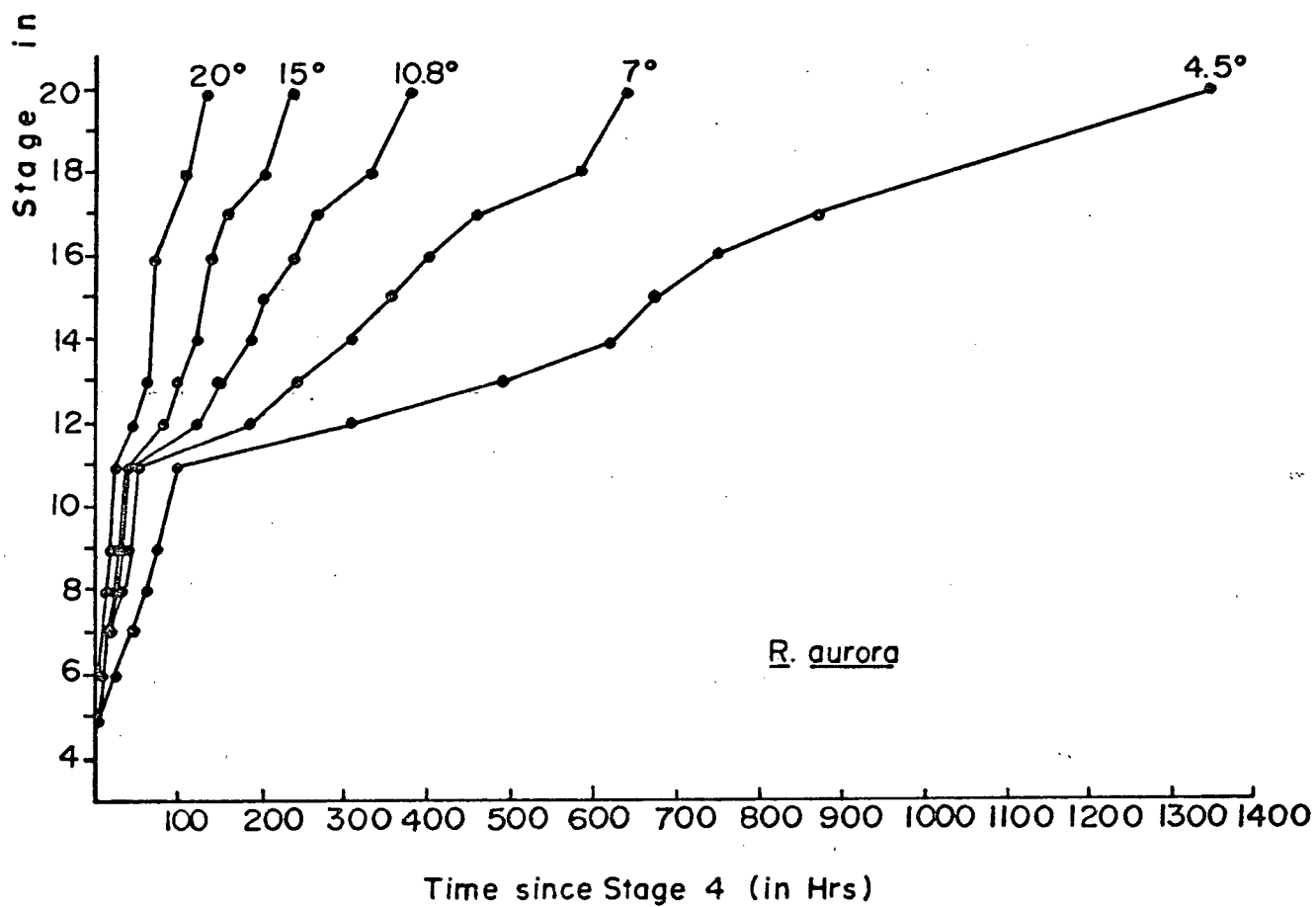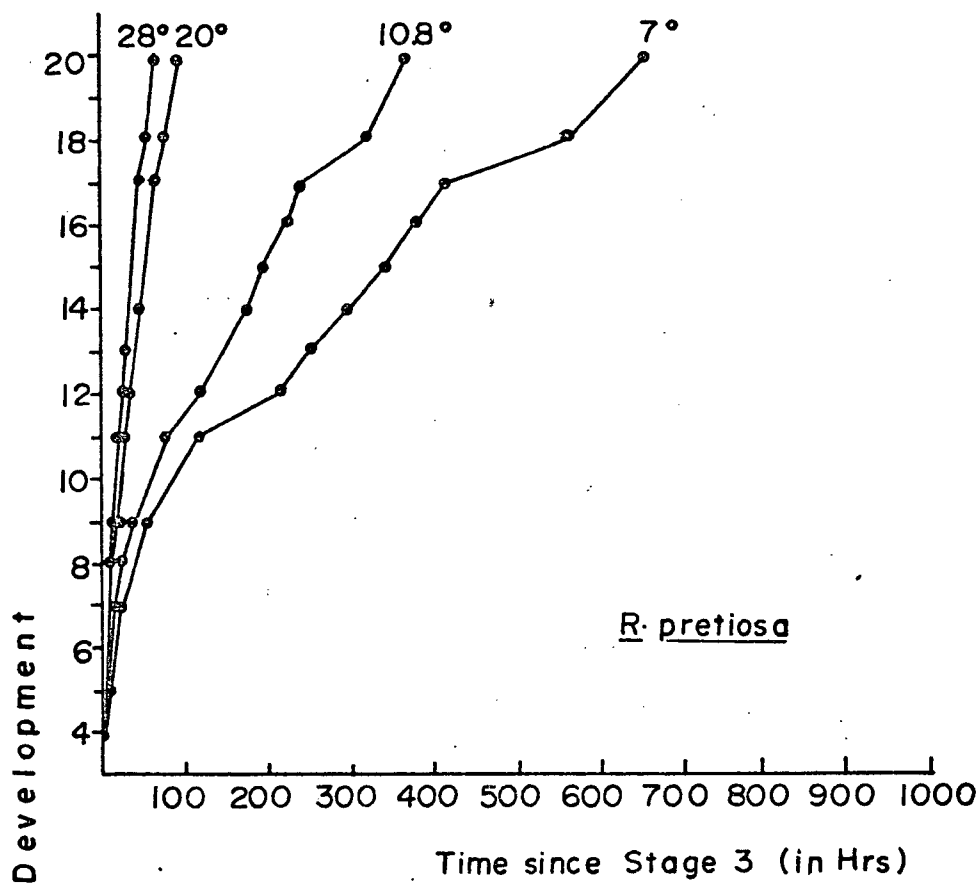
R. aurora

the upper limit is probably nearer 20 than 23 C. Thus the over-
all limits for R. aurora embryos in early stages are approximate-
ly 4-21 C.

Greater tolerance to temperature increase is gained as
development proceeds. Eggs first placed in 23 C at stage 11
were able to reach stage 20 successfully, although they did not
if maintained at this high temperature from an earlier stage.
Eggs in stage 9 could tolerate 21.5 C, but died in stage 17 at
both 26 and 28 C.

Embryos of R. aurora in stage 9 that were exposed to
1 C for either 2.5, 4, or 8 hours and subsequently kept in room
temperatures survived as well as control embryos. Survival was
over 80% for all groups.

The effect of temperature (within tolerable limits) on
the rate of development is seen in Fig. 25a. The biggest
increase in rates occur with only small increments of heat at
the lower end of the thermal limits, as can be seen by comparing
the slopes of the curves in Fig. 25a. This can be illustrated
another way by comparing the time for the eggs to reach stage 20
at each temperature. Based on the number of hours to reach
stage 20, the Q_{10} values can be calculated for various temper-
ature intervals (Table XXV).

As seen in Fig. 25a, the maximum delays in development
occurred between stages 11 and 12. Eggs at 1-3 C did not proceed
beyond stage 11, and at 4.5 C it took 210 hours for development
to proceed from stage 11 to stage 12. This delay was still
apparent at higher temperatures, although much diminished.

Embryos do not emerge from the jelly capsule until

TABLE XXV

Q_{10} values for embryonic development.

Temperature range C	Q_{10}
Rana aurora	
4.5 - 7.0	19.5
7.0 - 10.8	4.0
10.8 - 15.0	3.2
15.0 - 20.0	3.1
(10.8 - 20.0)	(3.1)
Rana pretiosa	
7.0 - 10.8	4.7
10.8 - 20.0	4.3
20 - 24	1.9
24 - 26	1.5
26 - 28	1.6
(20 - 28)	(1.7)

stage 21. They hatch with well developed gills and are capable of swimming, although they generally do not do so actively until after a few days.

The O_2 consumption by R. aurora embryos between stages 12-25 at 18.5 C averaged 0.59 cmm O_2/egg/hour (SD = .10), with a range of 0.51 to 0.77 cmm O_2/egg/hour, for the six replicates.

b. Rana pretiosa

The eggs of R. pretiosa are deposited in jelly masses that are rounded and globular, but less firm than those of R. aurora. Masses are laid in groups on top of or next to each other, unattached to vegetation and in only a few inches of water at the margins of the breeding sites. The diameter of 292 eggs from 12 masses averaged 2.31 (SD = .18) mm.

The percentage survival of embryos that successfully developed from stage 3 to stage 20 at each temperature is listed in Table XXIV. No development beyond stage 7 or 8 was noted for eggs at 1-3 C, and those at 4.5 C did not progress beyond stage 10 or 11. At 7 C, the survival was 76%. This may indicate that the lethal limit is at or not far below 6 C. Between 7 and 28 C, the embryos developed normally to stage 20.

The upper limit for development was determined by placing embryos at stage 5 in 30 C. They began showing abnormalities at stage 11, and most appeared as deformed neurulae in stage 14. About 55% reached stage 20, but all had warped backs and tails. Since these eggs were already in stage 5 when introduced to 30 C, and still did not survive, eggs in earlier stages would be expected to be even less tolerant. Hence, the

lethal limit for newly fertilized eggs (or those in stage 3) is probably close to 28 C. The maximum and minimum limits may be considered 6-28 C.

Embryos in stages 5 or 7 that were exposed to 1 or 3.5 C for either 2.5, 4, or 8 hours survived as well as did the controls.

The developmental rates at tolerable temperatures are seen in Fig. 25b. The curves for 24 and 26 C are intermediate to those for 20 and 28 C. Whereas an 8 C increase from 20 to 28 C only decreased the developmental time by 36%, the 3.8 C rise from 7 to 10.8 C decreased it by 44%, indicating that the eggs are most sensitive to small temperature changes at low temperatures. The variations in temperature sensitivity are also indicated by Q_{10} values based on the number of hours to complete development (Table XXV).

R. pretiosa embryos hatch in late stage 19, before they have attained gill circulation.

The O_2 consumption of embryos between stages 12 and 15 averaged 0.57 cmm O_2/egg/hour (SD = .06). The six replicates ranged from 0.50 to 0.69 cmm O_2/egg/hour.

c. Adult Spawning Behavior and Environmental Temperature

In the Lower Fraser Valley, both species begin breeding activities soon after ice melts from spawning sites. In 1968, 1969, and 1970, both species began breeding within the same week each year, when water temperatures in a temporary pond used for spawning reached 6 C.

The egg masses of both species are deposited in the

same pond or slow-moving river. However, there are important differences in breeding behavior. Male R. aurora are unique among all ranids in that they call under water. The males are submerged in the center of the pond, about 3 ft in depth, and up to 4 ft deep in the river, and call most actively at night. Female R. aurora are attracted to the males in these sites. They spawn only at night and place their eggs attached to vegetation at minimum depths of 18 inches, and at least 2 or 3 ft from the pond and river margins. Individual egg masses are about 2 ft apart. After a few days, some egg masses may break from their attachment and float to the surface.

Male R. pretiosa call in groups, with individual males only inches apart within the group. They call in air from the very margins of the pond and river in water only 2-6 inches deep. Most calling occurs in the daylight hours, and it is especially intense on sunny afternoons. R. pretiosa females spawn during the daylight, most often in full sunshine, and deposit their eggs at those sites where males call. Females tend to deposit their eggs on top of, or immediately next to, another egg mass, so that numerous masses may occur in an area less than 2 ft sq. The largest groups seen deposited in small areas were groups of 26, 19, and 11 egg masses; most others were from 5-8 masses. These egg masses are only in a few inches of water and the top halves of most are exposed directly to the air. Male R. pretiosa may call from the surface of the jelly masses once they are deposited, and consequently, females responding to their calls find masses nearby on which to deposit their own.

Whereas both species breed simultaneously when the

water temperature of the breeding pond has reached about 6 C
(in the center at a depth of 2 ft), and the eggs are laid on
the same days, the egg masses of each are subjected to very
different temperatures depending on where they are laid. Measure-
ments were made of the water temperatures actually surrounding
the eggs during their development in the field - water surround-
ing 18 R. aurora egg masses averaged 15.4 C (SD = 1.7) and 20.7 C
(SD = 2.7) around 19 R. pretiosa egg masses. (The measurements
were made at 1200 hr 3 cm away from each egg mass). The measure-
ments made only seconds apart indicate the divergent thermal
regimes to which the eggs are subjected. The data reflect the
differences that exist throughout the daylight hours. Almost
every day, R. pretiosa embryos develop in warmer water than
R. aurora embryos. There is less divergence at night, except
when near-freezing temperatures prevail.

The absorption of solar radiation by the black ova with-
in a jelly mass and the retention of this heat by the jelly
(Savage 1950), may raise the temperature within a mass above
that of the surrounding water. In full sunlight, during the
last week of March 1969, the temperatures within 16 R. aurora
masses averaged 15.3 C (SD = 2.2), while the surrounding water
averaged 13.8 C (SD = 2.1); the egg masses averaged 1.5 C
(range of 0.6 - 3.6 C) higher than the water. For R. pretiosa
the temperatures within 20 egg masses averaged 20.4 C (SD = 3.3),
while the surrounding water averaged 17.6 C (SD = 3.2). The
R. pretiosa egg masses averaged 2.7 C (range of 0.4 - 5.2 C)
higher than the water. The measurements were made in sunlight
so that the divergence between the water and internal mass

temperature is maximal. (A quick-reading thermometer was placed about 2 cm into the egg mass jelly, and the water reading was made about 3 cm from the mass). After dusk the jelly coats retain heat longer than the water does (4 R. pretiosa egg masses still had temperatures averaging 1.3 C higher than the water 1.5 hours after sunset), and only several hours after sunset do the mass and water temperatures become nearly the same. Metabolic heat from eggs may be retained by the jelly.

The internal temperatures of R. pretiosa egg masses diverge more from the water than do those of R. aurora masses. Because R. pretiosa masses are half exposed to the air by being in such shallow water, a great amount of jelly is exposed to direct sunlight, so that considerable heat is accumulated. Moreover, the grouping of the egg masses in one place also helps raise egg temperatures by reducing the flow of water around and through the masses; raised temperatures are maintained for longer periods in this fashion.

The R. aurora masses normally remain submerged while development proceeds, so that they are not exposed to direct sunlight. Those masses that float to the surface after breaking from their attachment to submerged vegetation are exposed to solar radiation on only a part of their dorsal surface. The compact, globular jelly mass allows only a small portion of jelly to become exposed to direct sunlight, but there is still enough heat gained to raise the internal egg mass temperature above that of water by as much as 3.6 C.

The highest temperature recorded within a R. pretiosa egg mass was 27.5 C, and the lowest was 4 C. However, on freezing

nights, which occurred on numerous occasions when eggs were still developing, the egg mass temperatures may have fallen below 4 C. Indeed, a thin layer of ice that had formed over the surface of the jelly masses overnight was seen on dawn visits to the study area in 1968 and 1969. In 1970, night temperatures were sub-freezing throughout most of the days the embryos were developing, and a large proportion of egg masses actually froze solid over-night; all frozen embryos died. On the other hand, almost every afternoon, the R. pretiosa masses reached 20 C and higher.

For R. aurora masses, the highest temperature recorded was 20.5 C, and the lowest was 4.5 C. Most daytime temperatures reached only 12-15 C within the masses, but freezing night temper-atures do not affect the masses deposited a foot or mor below the water.

DISCUSSION

Until this study, relatively little was known about the biology of R. aurora and R. pretiosa. These frogs are closely related and throughout their ranges they are almost completely allopatric. Consequently, the discovery of a sympatric locality provided a rare opportunity to study how they were able to coexist, since they were reported to resemble each other in habits. The mechanisms by which they achieve successful coexistence and avoid competitive exclusion were investigated.

This study has revealed that a primary ecological difference between the two species is that R. aurora is more terrestrial than R. pretiosa. Adaptations to their habitat preferences - land for R. aurora and water for R. pretiosa - provide the basis for a discussion of how these closely related species achieve successful coexistence.

A. Morphology

R. aurora and R. pretiosa are similar in general form and body size, but important morphological differences do exist. The length of the hind limbs differ. Those of R. aurora are longer than those of R. pretiosa of equal snout-vent length. The longer limbs of R. aurora correlate with its better capability at jumping; R. aurora can jump farther in distance and height than R. pretiosa. Rand (1952) found the same correlation when comparing the jumping abilities of six anuran species. In normal escape behavior, R. aurora usually jumps to flee from predators, and their leg morphology functions to this end. R. pretiosa uses swimming to escape from predators, and their

hind feet are extensively webbed. The basic habitat preference - land for R. aurora and water for R. pretiosa - are clearly reflected in the divergent adaptations of their limb morphology.

The position of the eyes also correlates with divergent behavior. R. pretiosa is more aquatic than R. aurora. The dorsal position of the eyes in R. pretiosa may function in several ways. In attempting to escape, these frogs normally submerge to the mud bottom of the river or rainpools. They remain on the bottom, usually with only their eyes exposed. The dorsal position of the eyes allows R. pretiosa to see while almost completely concealed in mud or debris. Moreover, as the frogs surface, they push their heads out of water, usually only their eyes and so expose only a small portion of their body to nearby enemies.

The eyes in the dorsal position may also help R. pretiosa in feeding activities, for frogs floating at the water surface, with only head and eyes showing, can remain hidden from nearby potential prey.

The coloration of R. aurora is adaptive in that the dorsal spots and brown-red background provide protection through disruptive coloration as the frog feeds and seeks escape in vegetation and plant cover on land. It is much more striking that the coloration of R. pretiosa is highly suited to its habitat preferences. The fairly uniform greenish-brown dorsum with disruptive black spots makes R. pretiosa very difficult to detect on the mud of the river banks or in the mud and debris at the bottom of the rainpools and river. The frog blends well with its background at essential times, during attempted escape

from predators, and when feeding.

The mucous covering on the skin of R. pretiosa becomes copious if the frog is handled. This results in the frog becoming very slippery and slimy enough to easily slip through one's grasp. This probably enables the frog to escape from some predators. This mucous may also function in water balance as discussed later.

B. Ecology

a. Food and Behavior

If competition is understood to be the demand for a resource available in limited quantities (Tanner 1967), then there is little likelihood of competition over food in the LCR study area. The field is rich in prey organisms suitable to both species; it is a rich area containing many diverse habitats. The availability of food is indicated by the fact that not a single frog of 145 examined was without food in its stomach. Moreover, no frogs caught during the study appeared weak and emaciated (except for a single blind R. aurora). Frogs that had never eaten external food were able to survive over one month without eating, and individuals starved that long would regain health and normal behavior when fed. Thus should a scarcity of food arise, an unlikely condition in the LCR study area, frogs of both species could withstand food limitations for many days.

In spring and autumn, when rainpools are filled, the frogs may feed closer to each other than at other times. Similar food will be encountered. As well as having different habitat preferences, the two species have different feeding

behavior. R. aurora moves around more to seek out food, while R. pretiosa waits to ambush its prey. Again, the opportunity for competition is limited because of divergent feeding tactics.

As in other aspects of their ecology, the species differ in the habitat preferred for daily feeding activities. R. aurora feeds predominantly on land, along the river bank or margins of rainpools, moving within the plant cover. R. pretiosa feeds almost exclusively from water. The food eaten reflects this divergence in feeding sites in that R. pretiosa eats more aquatic prey organisms than does R. aurora. The predominance of aquatic prey in the diet of R. pretiosa was also found in previous food studies (Schonberger 1945, Turner 1959).

Both species come into contact with many of the same prey items. The percentage overlap in their diet is high, especially between newly metamorphosed individuals, which feed within inches of each other during the summer months. Although both may feed on many of the same food items, they secure their food from a different substrate. Consequently, opportunities for direct competition of prey organisms are reduced. During wet weather, when both species feed on land, the chances of seeking food and competing are greater, but in most circumstances they will be separated by habitat preferences.

R. aurora has access to a wider variety of food, for they can take aquatic, semi-aquatic, and strictly terrestrial organisms during feeding sojourns. R. pretiosa is normally restricted to aquatic and semi-aquatic forms during most of the days, because of the warm dry weather which prevails during most of the summer. For example, they are not able to feed on the

terrestrial land slugs which are eaten abundantly by the R. aurora which finds them in the vegetation in the field.

b. Temperature Requirements and Adaptations

Temperature tolerance and preference of the frogs are additional factors which reduce potential competitive interactions between the species and allow greater niche partitioning and successful coexistence.

Frogs can regulate their body temperature to some extent by appropriate behavioral responses. By moving into or out of sunlight, or water, they can gain or lose heat accordingly. It is not likely that in natural conditions frogs will die from overheating. However, depending on their upper thermal tolerance, (below which they carry out daily life-sustaining activities), their activity will be modified. Frogs with high temperature tolerance are less subject to direct heat stress, and can also continue activities such as feeding, in conditions where frogs with lower thermal tolerance would be prevented.

R. pretiosa tolerates higher temperatures than does R. aurora. In the summer in the LCR study area, the air was often above 33 C. R. pretiosa can tolerate temperatures as high as 35 C, but R. aurora will die quickly above 33 C. Both species avoid high temperatures by moving into microhabitats which provide protection against heat stress. R. pretiosa uses water to thermoregulate, and it maintains a body temperature of about 27-30 C during very warm days. Lillywhite (1970) found that R. catesbeiana, a very aquatic frog, uses water to regulate its internal temperature also. Because R. pretiosa uses water for

feeding and other needs, during very hot days it can still remain active by remaining in the water. On warm days, insect activity is maximal and feeding behavior is intensive.

During hot days in July and August, R. aurora is not active in mid-afternoon when temperatures are high. Frogs restrict their movements to tangles of vegetation and shaded areas; they avoid open sunlight and increase their feeding about dusk. The few degrees difference in temperature tolerance between the two species, combined with their behavior in achieving preferred body temperatures, allows R. pretiosa to remain active when R. aurora is not. A few individuals of R. aurora had body temperatures of 28 C in hot days in July, but most were from 22-25 C. It was more common to find R. pretiosa with 27-30 C on these days. The difference in temperature tolerance and preference would reduce competitive interactions by allowing the frogs to be active at different times and places.

Heat stress is possible in the LCR study area for newly transformed R. aurora, which inhabit the pond. In July, when R. aurora metamorphose, the frogs find themselves in only a few inches of water at temperatures which can surpass their tolerance limits. They are forced to seek the cooler depths and cannot wander onto the vegetation, because of high air temperatures and reduced moisture available. Although they may not succumb, they are restricted to a habitat which allows maximal predation to occur. Snakes and invertebrate predators, especially Lethocerus, kill many of the transforming and new frogs. The tadpoles which have not yet metamorphosed probably do not escape from the many predators in the depths and consequently, most are probably eaten.

c. Water Requirements and Adaptations

It is difficult to say if R. pretiosa prefers the water, or is, indeed, restricted to it. There may be a subtle physiological basis underlying its very aquatic behavior, but studies on water balance did not reveal significant differences with R. aurora. Often R. pretiosa would submerge when it had caught a prey item, and they fed on land only in wet weather. Perhaps they can more easily digest food when it is moist. However, the necessity or preference for using water as a refuge from predators may also limit their choice of feeding sites. It would be advantageous feeding in places which leave an individual less susceptible to predation.

R. aurora and R. pretiosa lose water by evaporation at the same rate to still air. The rate of water loss is a function of body size, and frogs of small size lose water more rapidly than larger individuals. Adult body sizes of both species are about the same, with a maximum size of about 80 mm recorded for females. Young frogs differ in that R. aurora transform at a smaller size than R. pretiosa. R. aurora are 25-27 mm at metamorphosis, and at 28 C, such small animals desiccate rapidly, and die after a few hours with no opportunity to replenish lost water. This fact assumes importance, because at the time R. aurora metamorphose in the LCR study area, in July, temperatures are often above 28 C, and the only standing water is that of the river. R. aurora are restricted to the river margins, and are not active elsewhere in the field. This restriction to the river affects them in several ways. They are exposed to heavy predation by snakes and herons, which hunt along the river.

Also they are eaten by adult R. pretiosa, which feed from the
river, and eat small frogs when they can catch them. As soon as
the rains come in the fall, R. aurora move away from the river
to the rainpools.

Newly transformed R. pretiosa remain in the river
where they metamorphose. They find little restriction of their
movement since they prefer the aquatic habitat.

The body water content is the same for both species.
Each initially contains about 80% of body weight as water. This
is the same for other species of ranids studied (Thorson 1955).
Thus the time till death and the percentage water loss at the
lethal desiccation limit is not due to the initial water supply
of each species.

At 15 C, small frogs died when they had lost from
31-37% of their body weight, and the species did not differ. At
28 C, R. aurora lost an average of 29.7% of its body weight at
the critical activity point, and R. pretiosa lost 32.8%. The
temperature of 28 C is near the upper temperature tolerance
limit for R. aurora, and the heat stress may have influenced the
water balance. Thorson (1955) also found that R. pipiens died
after losing a smaller percentage of its body weight at near
lethal temperatures, than when desiccated at reduced thermal
conditions. For other species of North America ranids,
desiccated at moderate temperatures for each species, individuals
died after losing about 30-35% of their weight, as did R. aurora
and R. pretiosa.

R. aurora was more active in the cages while it was
being desiccated than was R. pretiosa. This may indicate that

R. aurora responds more quickly to water loss than does R. pretiosa, and actively seeks to find water to replenish losses. R. pretiosa assumed the water conserving position for longer periods than did R. aurora, but both species were very active when they had lost about 20% of their weight.

The copious amounts of mucous on the body of R. pretiosa should provide some defense against desiccation (Elkan 1968). In this respect, one would expect R. pretiosa to be more resistant to desiccation than R. aurora, which has less mucoid covering on its skin. Certainly, the extensive mucous on R. pretiosa would prevent body fluid dilution during the long intervals it remains in water, since it would effectively restrict abundant water inflow through its binding quality. The mucoid covering on the skin of R. pretiosa is probably adaptive in inhibiting water dilution since the species is so aquatic. (It also aids in escape behavior, because the frog, wet from its immersion in the river, becomes very slippery and can quickly squeeze out of one's hand).

The marked preference for water shown by R. pretiosa cannot be ascribed to an obvious physiological basis. Again, however, R. pretiosa moves to land only when the vegetation and ground are wet, (indicating water requirements as an underlying causal factor for its behavior). Perhaps because R. pretiosa is a poor jumper on land, when compared with R. aurora, it restricts its movements to moist locations. If it wandered far overland in dry conditions, it would face a danger of desiccation by not being able to return quickly and efficiently to water. It would be advantageous to venture onto land only

when the danger of dehydration is eliminated.

In contrast, R. aurora is a good, long, strong jumper, and quickly travels distances on land. It would have a better chance of finding water should the need arise, and as indicated by its greater level of activity in desiccation experiments, it would not wait for long periods before seeking to replenish lost water.

At 10 C frogs of both species survived equally well submerged in water for eight hours. It would be interesting to investigate their ability to remain submerged at higher temperatures, those normally found in summer conditions. At high temperatures, the rate of water flow across the skin should be increased, and oxygen in the water reduced. The mucoid covering on R. pretiosa skin may result in different capabilities under these conditions, preventing body fluid dilution while still allowing gas transport (Elkan 1968), while R. aurora may find difficulties.

d. Escape Behavior

The patterns of escape exhibited by frogs is species-specific and innate. Naive laboratory-reared frogs responded in threat situations as did wild caught frogs tested in the laboratory and observed in the field.

The circular jumping behavior of R. pretiosa released on land is intriguing. Because this species is rarely more than a few feet from standing water, jumping in a circular direction brings the frog into visual contact with water should it be forced away from it or lose its orientation. When R. pretiosa

begins its circular jumping pattern, it usually finds its way back to water after the first or second circles have been completed. These frogs hop low to the ground and soon tire if they have not been able to enter water. They apparently rely on their initial jumps to achieve their escape, and do not have the endurance to maintain saltatory behavior for long. Moreover, they are clumsy jumpers, and often trip on their webbed feet.

When R. pretiosa ventures onto land in wet and rainy conditions, it does not readily show the circular jumping pattern when frightened. The frogs hop directly and quickly to the nearest water; they apparently know their surroundings and the shortest route for escape to the nearest rainpool or river. Circular movements would not be advantageous, since a predator would easily capture the frog; the circular movement does not allow much distance to be gained. Clearly R. pretiosa is vulnerable on land and dependent on standing water for survival.

As Gans and Parsons (1966) noted, the important aspect of a frog's jumping ability is that it carry the frog across the water-land interface. In this respect, R. pretiosa can be considered a successful jumper. However, it is clear that R. aurora is more adept at jumping behavior, and indeed, depends on strong saltation for survival. The long, relatively straight jumps of R. aurora carry the frog many feet in a few seconds. Moreover, the angle of 45° at which R. aurora jumps is likely to yield the maximum flight distance for a given energy input (Gans and Rosenberg 1966). Another important feature of a high jump angle is that it allows a frog to leap over obstacles,

such as grasses and stems, that it may encounter along its
escape route. I saw this as I chased R. aurora in the field;
they moved quickly and efficiently over obstacles - sedges and
bulrushes - that would have blocked their path if they had not
cleared them with high jumps. The low jump angle of R. pretiosa
is inefficient in this respect; instead they rely on concealment
in grasses and plant cover, rather than jumping for flight, if
they are trapped on land and have not found water.

Both species rely on concealment and freezing against
the substrate for as long as possible before moving and ex-
posing themselves. R. pretiosa will wait until snakes approach
within inches before moving, but R. aurora jumps more readily.
This reflects the effectiveness jumping has for each species.
R. aurora is good and can elude a predator with a few long hops,
while R. pretiosa can not. On wet days, R. pretiosa was detected
on land only when they began rapidly jumping towards the river,
gambling to reach water before being caught as they jumped on
land. Of course, I cannot say how many R. pretiosa did not
jump as I neared them, but it can be concluded that water is
the refuge they prefer in their escape behavior, albeit, in
almost every other aspect of their behavior as well.

When R. pretiosa jumps into the water, it almost
always submerges into the mud bottom. In contrast, R. aurora
usually swam only a few inches out into the channel and then
clung to plants or floating debris. They did not remain in the
water for long, and rarely submerged. The presence of large
cutthroat trout in the Little Campbell River may be a reason
for this, and also small R. aurora could easily be eaten by

adult R. pretiosa which are found in the water.

C. Comparative Reproductive Behavior

a. Reproductive Isolation

In the LCR study area, both species begin breeding activity on virtually the same day of the year, and as seen in Tables XX and XXI, egg-laying may occur simultaneously. Both species breed in the same restricted portions of the pond and river. The mating call of both can be heard at the same time and place. Adult males of both species are 45-64 mm (sv length), and the females are 62-77 mm. Under these circumstances, one might expect a high percentage of interspecific matings. However, during both years, I found only one interspecific pair (a male R. aurora and a female R. pretiosa) in amplexus. The R. pretiosa was clasped on land as she moved to the breeding sites. Of more than one hundred egg masses studied, only a single egg mass may have resulted from a cross between R. pretiosa and R. aurora; the eggs were the size of R. pretiosa eggs. However, even this mass may not have been a bybrid one. It may have been a R. pretiosa egg mass destroyed in early developmental stages by cold temperatures. I have not crossed the species to determine the level of genetic compatibility, but it is unlikely that hybrid embryos will develop normally. Dumas (1966) and Porter (1961) have demonstrated that hybrid crosses of Pacific Northwest Rana do not produce viable off-spring, and they crossed both R. aurora and R. pretiosa with other species. Moreover, after examining several hundred frogs in the field, I have not found one resembling a hybrid or

difficult to identify as either species.

Thus there is no clear evidence for interspecific matings in these species that breed under conditions very susceptible to even chance encounters. Dozens of egg masses of each species were found within several feet of each other.

The following factors seem important for their successful reproductive isolation:

(1) The mating call of each is distinctive and as in other anurans (Littlejohn and Michaud 1959) the females are likely to respond to calls emitted by conspecific males.

(2) There are microgeographic differences in breeding sites. In the pond and river R. aurora breeds in water at least 3 ft from shore and in depth 12 inches and greater, while R. pretiosa breeds at the very edges of the river overflow and pond border in water only a few inches deep.

(3) R. aurora calls underwater, and R. pretiosa calls in the air.

(4) R. aurora calls mainly at night, and R. pretiosa calls mainly in the afternoon and evening, and rarely on warmer nights.

(5) R. aurora females probably respond to male calls only during the night and early mornings as they spawn only during the night. They spawn in deep water in areas where male R. aurora call. R. pretiosa spawn mainly during morning and mid-afternoon hours and in very shallow water in those spots where males have congregated.

(6) The effect of the single note uttered by amplectic

male R. aurora on the spawning behavior of the female is unknown. If it is a necessary part of the courtship behavior leading to successful egg-laying, a female R. aurora may be inhibited from releasing her eggs if clasped by a silent male R. pretiosa.

These factors work to reduce gamete wastage by restricting interspecific matings. Mayr (1963) has noted that ethological premating isolating mechanisms may be reinforced in the area of sympatry if compared to allopatric populations of each species. Blair (1955) has reported on such a finding in frogs of the genus Microhyla in the southwestern United States. However, referring to the reports of Storm (1960) for R. aurora in Oregon, and Turner (1958) for R. pretiosa in Wyoming, and the present work on populations of R. aurora in Stanley Park and Marion Lake, I find no major differences in behavior of these species in allopatric and sympatric populations. Nevertheless, differences may be subtle, and studies should be undertaken in this direction.

D. Embryonic Thermal Requirements

During the nonbreeding season, R. pretiosa is more aquatic than R. aurora. In almost all aspects of their ecology, R. pretiosa uses water and R. aurora uses land. During the breeding season, however, their behavior is reversed; R. aurora is more aquatic than R. pretiosa in that R. aurora spawns in the deep water of the pond and river whereas R. pretiosa breeds in water only a few inches deep at the very margin of the pond and river (Licht 1969b). This reversal presents certain problems, especially to the developing embryos. But in part, the embryos

are adapted to cope with some of these problems.

At each extreme, the thermal tolerance limits for R. aurora, 4-21 C, are beyond those encountered by developing embryos. R. aurora usually do not spawn until the water reaches 6 or 7 C. After this temperature is reached only an unusually prolonged cold spell could lower the temperature at the depths the eggs are deposited to below 4 C. Moreover, the embryos can withstand short-term cold exposure as low as 1 C. The egg masses are completely submerged and so well protected from thermal extremes. Even those masses that rise to the surface do so only after the embryos are at stages where they can tolerate temperatures beyond 21 C. Female R. aurora spawn at night and the eggs are not exposed to sunlight and rising temperatures until several hours after fertilization. This means that the embryos have progressed several stages before water temperatures rise, and their tolerance is increased. For example, embryos in stage 4 can tolerate 20 C but not 23 C, however, embryos in stage 9 can survive at 23 C. Survival after short-term exposure in even higher temperatures is likely. (A detailed discussion of breeding habits and embryonic thermal requirements is found in the paper by Licht (1970)).

For R. pretiosa, the upper limit of 28 C is sufficiently high to provide safety from most natural heat stress. However, freezing and subfreezing night temperatures, that often occur during February and March in the Lower Fraser Valley, present a major problem. Although young embryos can withstand temperatures as low as 1 C for at least up to eight hours (a longer interval of low temperatures than normally occurs in the

field), subfreezing temperatures in the field may result in ice formation on the dorsal portion of the grouped egg masses. Ice destroyed whole egg masses in 1970.

Embryos of both species are responsive to small changes in temperature at the lower end of their tolerance limits: i.e. Q_{10} values are highest at low temperature intervals. This rapid acceleration in developmental rates with only small increments of heat has the important advantage of minimizing any delay in development due to cold. Both species breed in temporary ponds, and if these dry up before the tadpoles metamorphose, the frogs are left stranded. The quicker the hatching time, the sooner the tadpoles can assume growth toward metamorphosis. In addition, ranid eggs are palatable and nontoxic when eaten by possible predators (Licht 1969c). Prolonged delays in development could result in more predation on the relatively defenseless embryos.

Because of the relatively exposed site of the egg masses of R. pretiosa, embryos of this species are subjected to both higher and lower temperatures than those of R. aurora. For R. pretiosa, time to complete development is decreased by 71% between 10 and 20 C, but only by 36% between 20 and 28 C. The Q_{10} values within any interval between 20 and 28 C are about the same. This means that once a minimum temperature of 20 C is attained within the R. pretiosa egg mass, there is little further gain in developmental rate. The pattern of grouping the egg masses in very shallow water results in temperatures within masses reaching 20 C or more almost daily, so that development during daylight proceeds maximally. By spawning in

the early morning or mid-day, often in full sunlight, females immediately provide warm temperatures for newly fertilized eggs. The shallow water warms quickly and remains so for several hours after dusk. Embryos can undergo several hours of rapid development before being exposed to the cold night temperatures. Apparently the R. pretiosa population of the Lower Fraser Valley uses all possible heat sources during the daylight to achieve maximal embryonic developmental rates. Although even young embryos can tolerate temperatures as low as 1 C for several hours, the daylight spawning of R. pretiosa appears to be an adaptation for ensuring the embryos are at an advanced stage before exposure to possible lethal cold temperatures.

Although the data on O_2 consumption of embryos in late gastrulation (stage 11) show no significant differences between the two species, there may be differences in later stages of development. Since R. aurora embryos hatch at stage 21 and R. pretiosa hatch in late stage 19, this difference may reflect a difference in O_2 requirements of the advanced embryos (Moore 1940). The cool deep waters where R. aurora embryos develop are rich in oxygen. An oxygen-rich environment allows the embryos to hatch at a relatively late, free-swimming stage. However, R. pretiosa embryos develop in the warm, shallow, oxygen-deficient margins of the pond and river. Frog embryos consume more O_2 as they develop (Moog 1944). The O_2 present in the warm water is probably sufficient for the early stages, but may be insufficient as the embryos near hatching. Since the jelly surrounding the eggs reduces the diffusion of oxygen from the water to the embryo, it is advantageous under low oxygen

conditions for the embryos to hatch at an early stage.

The poor embryonic survival of R. pretiosa compared with that of R. aurora may be indirectly a result of oxygen deficiency. There is very little water flow in the places where R. pretiosa embryos develop, especially in the pond. Bacteria, algae, and fungi are not washed away and tend to coat most of the egg masses. Embryos were seen moving inside fungus-covered eggs, but were dead several days later, presumably smothered by the fungus coating. The better survival of R. pretiosa in the river compared with the pond in 1968 is probably because of better water flow over the eggs in the river.

R. aurora is clearly a species adapted to breed in 'northern' environments. The breeding behavior, characteristics of the eggs and egg masses, the low minimum and maximum temperature tolerance, and the late stage of hatching, all function for developmental success of embryos in cool waters. Only the developmental rates are slow when compared with those of other 'northern' species.

R. pretiosa is peculiar in several respects. Females spawn on the same dates as R. aurora females, but they do not provide a 'northern' environment for their eggs. Since the egg masses are in clusters in a few inches of water at the margins of breeding sites, heat is trapped and the internal temperatures of the egg masses are raised. As a result development proceeds maximally during the day. However, this gain in increased rates is offset by two major factors. First is the low night temperatures (already discussed), that are capable of

destroying many embryos , particularly those at the surface of exposed masses.

The second disadvantage may be even more important. In the Lower Fraser Valley, only a few days without rain, results in a appreciable drop in the margins of the slow-moving streams and ponds where both species spawn. For R. aurora this presents little problem, as its eggs are at least several feet away from the water's edge and in deeper water. However, the eggs of R. pretiosa are often left stranded by the receding water, and entire egg masses may be desiccated.

The populations of R. pretiosa west of the Coastal mountains, such as the study population, reached the Lower Fraser Valley postglacially either from Central British Columbia or from the east (Dumas 1966). The main continuous range of R. pretiosa lies east of the Coast mountains. In one population from within the continuous range of this species (7800 ft in Wyoming), R. pretiosa is reported to lay eggs in groups at the margins of temporary ponds (Turner 1958). Apparently the Lower Fraser Valley population of R. pretiosa has not evolved new breeding habits, and has retained the same reproductive behavior as populations to the east. Their 'strategy' seems to be that of racing against high mortality from cold at night, and desiccation in dry spells, by using available heat during the day to increase developmental rates and thereby decrease the time till the embryos hatch. This 'strategy' appears marginal in my study area, and R. pretiosa suffers high pre-hatching mortality when compared with R. aurora.

The only data available on temperature tolerance of

R. pretiosa from east of the Coastal mountains is that of
Johnson (1965). He recorded thermal limits of 6-28 C for
R. pretiosa lutiventris embryos. If this is typical of eastern
populations, it appears that the reproductive 'strategy' and
thermal tolerances of R. pretiosa are the same throughout its
range. This does not mean that the 'strategy' is marginal
throughout its range. In the Lower Fraser Valley R. pretiosa
may be prevented from evolving better adapted breeding behavior,
such as spawning in deeper water, by the presence of R. aurora.
Successful reproductive isolation between these two species is
due in part to their specific choice of spawning sites. A
change to deeper water spawning by R. pretiosa would probably
result in a breakdown of the reproductive isolating mechanisms
that separate it from R. aurora. In such a case, the loss of
reproductive effort and the resulting embryonic mortality would
probably be greater than the mortalities now due to desiccation
and freezing.

E. Coexistence of Ranid Frogs in the Pacific Northwest

The most important point brought out by the invest-
igation of the comparative ecology of the two species of frogs
is that R. pretiosa is more aquatic than R. aurora. In almost
all aspects of its ecology, R. pretiosa used water, either by
preference or restriction, while R. aurora used land. The basis
of their ecological separation is the water-land boundary. This
is true whether the body of water is a small rainpool, the pond,
or the river. R. pretiosa is almost always found in the water,
floating on the surface in mid-stream or at the water margins.

R. aurora is found on land, perhaps at the water edge, but most often several feet inland.

The obvious preference or restriction to water for usual daily activities shown by R. pretiosa is probably the major factor allowing successful coexistence with R. aurora. As a consequence of their divergent habitat preferences, competitive interactions severe enough to lead to exclusion of either species are not operating in the LCR study area. The only adverse effect of the two species living in sympatry dis- covered in this study is the possible predation of small R. aurora by adult R. pretiosa, especially during the summer when both species live in or along the river. The population size of each species is not greatly affected by the other's presence.

The distributions of the species, and their rare occurrence in sympatry, are not explained by competitive inter- actions, a possibility which existed before this study. R. pretiosa can be successful and establish large populations within the range of R. aurora. The Coast Range mountain Chain undoubtedly is a barrier for more extensive intermingling of the species on a broad scale. However, local habitat condi- tions will most likely determine whether either species will survive in a particular locality.

There are certain requirements of a habitat should it be occupied by either R. aurora or R. pretiosa. The embryonic requirements, those of the eggs and developing embryos, are important in controlling their distributions. For R. pretiosa there must be sufficient rainfall during the breeding season

so that the egg masses are not left stranded on the banks of the bodies of water used as spawning sites. In the Lower Fraser Valley, spring rains are usually abundant, but if not, R. pretiosa may lose a full year's reproductive output.

For R. aurora, the breeding sites must be of sufficient depth so that the eggs are not exposed to undue heat stress as the embryos have a very low heat tolerance (Licht 1970). R. aurora deposit their eggs in such a manner that they will not be stranded under conditions of sparse rainfall.

For non-breeding R. pretiosa, an essential habitat requirement is the presence of standing water. The feeding and escape behavior of R. pretiosa are carried out almost entirely in standing water, and the species would not survive without it. R. aurora is able to live away from standing water by moving into wooded areas, which provide conditions to meet their needs during non-breeding activities. They can seek escape from high temperatures, and in woods, high humidities prevail. However, if standing water is present, R. aurora also depends on it for food and escape. But they are not as dependent as R. pretiosa.

There are no obvious reasons why R. pretiosa is so scarce west of the Coast Range, especially in the Lower Fraser Valley. In this locality there exist many areas which meet the requirements of R. pretiosa; indeed, R. aurora is widespread in these places. There is one strong possibility to explain the scarcity of R. pretiosa. Bullfrogs, Rana catesbeiana, were introduced into the Lower Fraser Valley about 100 years ago. They have since successively established large populations and are widespread throughout the Lower Fraser Valley.

Rana catesbeiana is a highly aquatic frog, and like R. pretiosa, is restricted to water or its immediate vicinity all year round. Moreover, R. catesbeiana is a voracious predator and often feeds on other anurans; bullfrogs are the largest anurans in North America and can feed on adult frogs of most other species. It would eat R. pretiosa juveniles, and probably even the adults (certainly males) with little trouble. Thus it is highly likely that R. pretiosa was once more widespread in Lower Fraser Valley before the bullfrog was introduced. Dumas (1966) found that in western Washington R. pretiosa populations were threatened by enlarging R. catesbeiana populations and may now be extinct.

Further evidence for this hypothesis is the following finding. About three miles to the west of the LCR study area, downstream on the Little Campbell River, is a locality where R. catesbeiana are found in large number They are sympatric with R. aurora. The habitat conditions in that area are sufficient to meet the requirements of R. pretiosa, but this species is absent from the area. It would be only years before R. pretiosa would be eliminated from such an area, having to feed in ponds and streams side by side with the much bigger, highly predatory bullfrog.

In 1970, the first bullfrogs were found in the LCR study area. They probably migrated from lower portions of the river. Thus, in a matter of years, the R. pretiosa population may be in danger of elimination from the LCR study area. I believe it to be an unfortunate way of testing the above hypothesis, but the changing numbers of R. pretiosa in future

years will be worth watching closely.

The ecological equivalent of R. aurora east of the Coast Range in British Columbia is the wood frog, R. sylvatica. It is much like R. aurora in its preference for land over water for non-breeding activities (Heatwole 1965, Bellis 1966). R. pretiosa and R. sylvatica are sympatric throughout eastern British Columbia. R. aurora may indeed be excluded from eastern B.C., because of competition with R. sylvatica. The red-legged frog can coexist with either the bullfrog or the western spotted frog, which are highly aquatic forms, and either of these latter two frogs could coexist with the wood frog. But neither R. aurora and R. sylvatica or R. pretiosa and R. catesbeiana species pairs would survive in sympatry.

LITERATURE CITED

Bellis, E.D. 1965. Home range and movement of the wood frog in a northern bog. Ecology 46: 90-98.

Blair, W.F. 1955. Mating call and stage of speciation in the Microhyla olivacea-M. carolinensis complex. Evolution 9: 469-480.

Bogart, C.M. 1960. The influence of sound on the behavior of amphibians and reptiles. In Animal Sounds and Communication. Edited by W.E. Lanyon and W.N. Tavolga. Amer. Inst. Biol. Sci., Washington, D.C. p. 137-320.

Brown, H.A. 1967. High temperature tolerance of the eggs of a desert anuran, Scaphiopus hammondi. Copeia, 1967: 365-370.

Carl, G.C. 1966. The amphibians of British Columbia. Brit. Columbia Prov. Mus. Handbook No. 2: 1-62.

Carl, G.C. and I. McT. Cowan. 1945. Notes on some frogs and toads of British Columbia. Copeia, 1945: 52-53.

Cowles, R.B. and C.M. Bogart. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. 8: 256-296.

Dumas, P.C. 1966. Studies of the Rana species complex in the Pacific Northwest. Copeia, 1966: 60-74.

Elkan, E. 1968. Mucopolysaccharides in the anuran defence against desiccation. J. Zool. London, 155: 19-53.

Gans, C. and T.S. Parsons. 1966. On the origin of jumping mechanisms in frogs. Evolution 20: 92-99.

Gans, C. and H.I. Rosenberg. 1966. Numerical analysis of frog jumping. Herpetologica, 22: 209-213.

Gause, G.F. 1934. The struggle for existence. Williams and Wilkins. Baltimore.

Heatwole, H. 1961. Habitat selection and activity of the wood frog, Rana sylvatica Le Conte. Amer. Midl. Nat. 66: 301-313.

Heatwole, H., F. Torres, S. Blasini de Austin, and A. Heatwole. 1969. Dynamics of evaporative water loss by the coqui, Eleutherodactylus portoricensis. Comp. Biochem. Physiol. 28: 245-269.

Holmes, R.T. and F.A. Pitelka. 1968. Food overlap among co-existing sandpipers on northern Alaskan tundra. System. Zool. 17: 305-318.

Hutchison, V.H. 1961. Critical thermal maxima in salamanders. Physiol. Zool. 34: 92-125.

Jenssen, T.A. and W.D. Klimsta. 1966. Food habits of the green frog, Rana clamitans, in southern Illinois. Amer. Midl. Nat. 76: 169-182.

Johnson, O.W. 1965. Early development, embryonic temperature tolerance and rate of development in Rana pretiosa lutiventris Thompson. PhD Thesis. Oregon State Univ. (Diss. Abst. 25).

Lack, D. 1945. The ecology of closely related species with special reference to cormorant (Phalacrocorax carbo) and shag (P. aristotelis). J. Anim. Ecol. 14: 12-16.

Licht, L.E. 1969a. Unusual aspects of anuran sexual behavior as seen in the red-legged frog, Rana aurora aurora. Can. J. Zool. 47: 505-509.

Licht, L.E. 1969b. Comparative breeding behavior of the red-legged frog (Rana aurora aurora) and the western spotted frog (Rana pretiosa pretiosa) in south-western British Columbia. Can. J. Zool. 47: 1287-1299.

Licht, L.E. 1969c. Palatability of Rana and Hyla eggs. Amer. Midl. Nat. 82: 296-298.

Licht, L.E. 1970. Breeding habits and embryonic thermal requirements of the frogs, Rana aurora aurora and Rana pretiosa pretiosa in the Pacific Northwest. Ecology 52: 116-124.

Lillywhite, H.B. 1970. Behavioral temperature regulation in the bullfrog, R. catesbeiana. Copeia 1970: 158-168.

Littlejohn, M.J. and T.C. Michaud. 1959. Mating call discrimination by females of Strecker's chorus frog (Pseudacris streckeri). Tex. J. Sci. 11: 86-92.

MacArthur, R.H. 1958. Population ecology of some warblers of northern coniferous forests. Ecology 39: 599-619.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge.

Moog, F. 1944. The chloretone sensitivity of frogs' eggs in relation to respiration and development. J. Cell. Comp. Physiol. 23: 131-155.

Moore, J.A. 1940. Adaptive differences of the egg membranes of frogs. Amer. Naturalist, 74: 89-93.

Moore, J.A. 1949. Pattern of evolution in the genus Rana. In Genetics, paleontology and evolution. Edited by Jepsen, G.L.E., Mayr, E. and Simpson, G.G. Princeton Univ. Press, N.J. p. 315-338.

Pollister, A.W. and J.A. Moore. 1937. Tables for the normal development of Rana sylvatica. Anat. Rec. 68: 489-496.

Porter, K.R. 1961. Experimental crosses between Rana aurora aurora Baird and Girard and Rana cascadae Slater. Herpetologica, 17: 156-165.

Rand, A.S. 1952. Jumping ability of certain anurans, with notes on endurance. Copeia 1952: 15-20.

Schonberger, C.F. 1945. Food of some amphibians and reptiles of Oregon and Washington. Copeia, 1945: 120-121.

Spight, T.M. 1968. The water economy of salamanders: evaporative water loss. Physiol. Zool. 41: 195-203.

Storm, R.M. 1960. Notes on the breeding biology of the red-legged frog (Rana aurora aurora). Herpetologica, 14: 96-100.

Stebbins, R.C. 1951. Amphibians of Western North America. Univ. of Calif. Press, Berkeley.

Stebbins, R.C. 1954. Amphibians and Reptiles of Western North America. McGraw-Hill, N.Y.

Tanner, J.T. 1966. Effects of population density on growth rate of animal populations. Ecology 47: 733-745.

Thorson, T.B. 1955. The relationship of water economy to terrestrialism in amphibians. Ecology 36: 100-116.

Turner, F.B. 1958. Life history of the western spotted frog in Yellowstone National Park. Herpetologica, 14: 96-100.

Turner, F.B. 1959. An analysis of the feeding habits of Rana pretiosa pretiosa in Yellowstone National Park, Wyoming. Amer. Midl. Nat. 61: 403-413.

Turner, F.B. 1960. Population structure and dynamics of the western spotted frog, Rana pretiosa pretiosa Baird and Girard in Yellowstone Park, Wyoming. Ecol. Monog. 30: 251-278.