

## Comparative life history features of the western spotted frog, *Rana pretiosa*, from low- and high-elevation populations

LAWRENCE E. LICHT

Department of Biology, York University, 4700 Keele Street, Downsview, Ontario M3J 1P3

Received March 12, 1975

LICHT, L. E. 1975. Comparative life history features of the western spotted frog, *Rana pretiosa*, from low- and high-elevation populations. *Can. J. Zool.* **53**: 1254–1257.

Comparisons are made of life history features of the western spotted frog, *Rana pretiosa pretiosa*, living at 70 m in southwestern British Columbia, and 2600 m in Yellowstone Park, Wyoming.

Lowland tadpoles remain longer as larvae and transform at twice the body size as highland tadpoles.

Growth rates of juveniles and adults are rapid in the lowland population and the same amount of growth achieved by them in 2–3 years takes 8–10 years for highland frogs.

Body size at sexual maturity is the same for frogs from both populations, but B.C. frogs breed at half the age of Wyoming frogs. Female fecundity, the number of eggs at spawning, is the same, but lowland females breed annually, while high-elevation females breed only every 2 or 3 years.

Various explanations are put forth to account for observed differences.

LICHT, L. E. 1975. Comparative life history features of the western spotted frog, *Rana pretiosa*, from low- and high-elevation populations. *Can. J. Zool.* **53**: 1254–1257.

On a comparé certains aspects du cycle vital chez des grenouilles de l'ouest *Rana pretiosa pretiosa* vivant à une altitude de 70 m dans le sud-ouest de la Colombie Britannique et à une altitude de 2600 m dans le Parc Yellowstone au Wyoming.

Les têtards en basse altitude restent à l'état larvaire plus longtemps et se transforment en adultes lorsqu'ils ont atteint deux fois la taille des têtards de haute altitude.

Les taux de croissance des jeunes et des adultes sont rapides dans la population de basse altitude et la croissance effectuée par cette population en 2 ou 3 ans requiert 8–10 ans chez les grenouilles de haute altitude.

La taille à la maturité sexuelle est la même chez les deux populations, mais les grenouilles de Colombie Britannique se reproduisent à la moitié de l'âge des grenouilles du Wyoming. La fécondité des femelles et le nombre d'œufs à la ponte sont les mêmes, mais les femelles des terres basses se reproduisent chaque année, alors que celles de haute altitude se reproduisent seulement tous les 2–3 ans.

On propose plusieurs théories pour expliquer les différences observées.

[Traduit par le journal]

### Introduction

Parameters such as female fecundity, larval, juvenile, and adult growth rates, and age at maturity are major components of a species' life history and have much influence on overall population dynamics and structure (Cole 1954; Gadgil and Bossert 1970). These characters, like other life history features, are adapted to local environmental conditions, and Ehrlich and Raven (1969) have suggested that a species be viewed as a mosaic of populations, each of which may be highly divergent in important life history traits.

Studies on amphibians have shown that populations of a single species at different altitudes may be very different in egg size (Pettus and Angleton 1967), egg developmental rates (Ruibal 1955), and age at maturity (Tilley 1973).

A detailed study of the ecology of the western spotted frog, *Rana pretiosa pretiosa*, was made in marshes at 70-m elevation in southwestern British Columbia. Results were compared to those from similar work (Turner 1958, 1960a) done on the same species living at 2600 m in Wyoming, and remarkable differences in certain life history features were discovered.

### Methods

A detailed description of the study area, Little Campbell River in B.C., can be found elsewhere (Licht 1974). Data presented here were collected by use of a mark-recapture program carried out from 1967 to 1970. All frogs caught were individually marked by toe-clippings, and upon capture and each recapture the snout-vent length was measured to the nearest millimetre. Sex and maturity as indicated by secondary sex characters were recorded. Throughout the study 628 frogs were marked and there were 437 recaptures.

TABLE 1

Comparative life history features of *Rana pretiosa* living at 70 m along the Little Campbell River in British Columbia and at 2600 m in Yellowstone Park, Wyoming\*

	LCR		Wyoming
Tadpole size at hatching, mm	12		10
Maximal total length of tadpole, mm	90		60
Size at transformation, mm	33		16
Duration of larval life (range in days)	110-130		70-85
Growth of frogs in first full year (initial and final size in mm)	38-58	Males	24-33†
	38-62	Females	
Growth of frogs in second full year (initial and final size in mm)	58-64	Males	33-40†
	62-77	Females	
Size at sexual maturity, mm	45	Males	ca. 45
	62	Females	ca. 60
Age at sexual maturity, yr.	2	Males	4
	2-3	Females	6
No. of eggs in spawn	643 (249-935)		539 (206-802)
	(n = 18)		(n = 16)
Breeding cycle for females, yr.	1		2-3

\*Data on Wyoming frogs from Turner (1958, 1960a).  
 †Data for male and female frogs combined.

All data for the highland *Rana pretiosa* come from work by Turner (1958, 1960a).

**Results**

In both highland and lowland localities, *R. pretiosa* breed as soon as ice melts from water used as spawning sites. The adult breeding behavior appears identical in both areas (Turner 1958; Licht 1969, 1971).

A summary of comparative life history features can be seen in Table 1. Data for Wyoming frogs are averages compiled by Turner (1960a). Sizes given for Little Campbell River frogs are also averages of growth of 50-150 frogs in each age class. All data from both localities are based on measurements from recaptured frogs.

The number of eggs laid by a female does not differ significantly between populations. However, in lowland B.C., females breed every year while in Wyoming, females breed only every 2 or 3 years.

Tadpoles hatch at almost the same size but lowland tadpoles grow much larger and remain in the aquatic environment over a month longer than those in Wyoming. At transformation, Little Campbell River frogs are about twice as large as those in Wyoming. During the year of transformation, lowland frogs grow from 33 to 38 mm and Wyoming frogs from 16 to 24 mm. Growth during the next 2 years is shown in Table 1. After the 3rd year, frogs in the Little Campbell River are almost maximum size and

do not grow at all or at most 1 mm a year. In Wyoming, growth after the 3rd year continues but is slow: 3rd year, 40-45 mm; 4th year, 45-50 mm; 5th year, 50-53 mm. After the 5th year, growth is slower and frogs reach maximum size after 8-10 years. In Wyoming, females grow to 72 mm, males to 61 mm. Lowland females grow to a maximum of about 78 (two females were 80 mm) and males to 64 mm. In both localities sexual maturity is reached at the same body size, about 45 mm for males and about 60 for females, but this size is reached in half the time by lowland frogs (Table 1).

**Discussion**

The possibility that the Wyoming and Little Campbell River frogs are not the same species should be mentioned. However, evidence that they are the same, as currently recognized, is strong. Pigmentation is identical, and habitat preference and male and female breeding behavior, including oviposition site, vocalizations, and spawning behavior, appear identical.

In the Little Campbell River, *Rana pretiosa* occurs with a closely related frog, *Rana aurora*. The growth of *R. aurora* was studied in the Little Campbell River and in another lowland locality where only *R. aurora* is found. No difference in life history features was noted indicating that *R. pretiosa* has little obvious effect on growth rates of *R. aurora*. It will be assumed, then, that

the growth observed in *R. pretiosa* in the Little Campbell River has not been markedly influenced by some potential competitive interaction with *R. aurora*, although the possibility does exist.

The disparity in growth rate and age of maturity is extreme between populations. In Wyoming, the largest females are about 70 mm and 9 or 10 years old, and Turner (1960a) states "it is hard to imagine the attainment of such a size any sooner." Eight or 9 years are needed by males to reach 57 mm in Wyoming. Thus, the amount of growth taking 8–10 years in Wyoming is reached in 2 years in the Little Campbell River. Prereproductive life is greatly protracted in Wyoming.

The most obvious explanation for this marked delay of growth and sexual maturity is environmental differences. In the lowland habitat, frogs are active from February through October, while in Wyoming they are active only from May through August. In Wyoming the mean annual temperature is 0.1°C and the high is 13.4°C in July. In the Little Campbell River, the mean annual temperature is 10°C and the high, also in July, is 27.7°C. Most months and days are warmer in the lowland environment, thus permitting greater frog activity and consequent feeding and growth.

Although environmental temperatures and length of growing season seem important for adult growth, larval growth differences may be more complex. In both the Little Campbell River and Wyoming study areas, tadpoles live in predominantly temporary ponds, but there is permanent water available for them in the lowland habitat. Temperatures in the highland aquatic habitats are colder than in the lowland and undergo wider diurnal variations (Turner 1958). The larval growth differences observed are likely a consequence of different water temperatures and permanency of water, but genetic influences cannot be dismissed. Tadpoles in Little Campbell River spend over a month longer in the aquatic habitat and as a consequence are twice as large as Wyoming frogs at transformation. This increased size at transformation reduces the age at which mature body size is attained by a full year for lowland frogs, while Wyoming frogs must grow on land for another 2 years to reach the same size.

The extent to which genetic factors influence growth rate of larvae and adults cannot be determined and environmental differences may mask

an important genetic divergence. A rewarding study could be accomplished by transplanting individuals—eggs, tadpoles, and adult—to alternate localities or to simply raise individuals from the Little Campbell River and Wyoming under identical lab conditions.

Whether differences in growth are genetic or not, the differences in the two populations of *R. pretiosa* tend to fit a general theory of adaptive nature of life history recently discussed by Tilley (1973). The theory predicts that delayed maturity should be adaptive in relatively stable environments, but that it will be disadvantageous in environments in which periods of increase in population numbers are interspersed with brief periods of heavy mortality or reproductive failure.

In Wyoming, there are fewer predators on *R. pretiosa* than in the Little Campbell River where predators on anurans abound (Licht 1974). However, estimates of adult survival do not differ markedly, being 61% in Wyoming and 65% in the Little Campbell River. A crucial difference between the populations is that in the lowland area, the entire reproductive effort during a year may be lost. In the Little Campbell River, *R. pretiosa* lay eggs in very shallow margins of the pond and river. After a few days of no rain the eggs are stranded. In 1969, all embryos would have died had they not been moved to water (Licht 1971). In Wyoming, there is heavy larval mortality (as the case seems to be for most temperate-zone anurans) but it is not likely to be total as in the Little Campbell River.

As the theory predicts (Tilley 1973), if the population is subject to brief periods of reproductive failure (such as the total failure for Little Campbell River frogs), then delayed maturity is disadvantageous. If the population is relatively stable, as in Wyoming, delayed maturity can be a benefit, by permitting larger growth and subsequent greater fecundity before females breed. In Wyoming, females do not breed every year and they first breed when large. Fecundity is positively correlated with body size (Licht 1974). The same numbers of eggs are laid by females in both populations, but in the lowland, females breed annually. This is probably due to longer feeding activity permitted lowland females; more energy can be directed toward ova production. There is probably a vast difference in energy available for partitioning to ova by lowland and highland individuals and this problem is worthy of study. The differences in

available energy make it difficult to compare fecundity in lowland and highland females.

In Wyoming, delayed maturity is not disadvantageous because embryonic survival is not so overwhelmingly threatened as in the Little Campbell River. In Wyoming, as in the Little Campbell River, larval mortality may be low or even total at times, but in the Little Campbell River it is embryonic mortality which can be 100% and thus precludes any chance of larval transformation and population recruitment. Three or 4 years of little or no rain after eggs are laid in a season would drastically reduce population numbers and could possibly exterminate the lowland population.

The last statement brings up a pertinent point, that of longevity. A long-standing question is whether relative differences in metabolic rates result in different life spans (Pearl and Miner 1935). The slower-growing Wyoming populations are definitely long-lived and although age span is not known for the lowland individuals, according to Pearl and Miner (1935) they would not be expected to have as long a life span as the highland populations. After 3 years, females in the Little Campbell River are virtually at maximum size, that reached in nearly 10 years in Wyoming. If lowland individuals do not live long after maximum growth, then as pointed out earlier, 3 or 4 years of no recruitment to the population may be disastrous. In the highland population, long-lived breeding individuals would be greater insurance against poor recruitment in successive years and possible local population extinction.

In summary, *R. pretiosa* in the Little Campbell River is adapted to overcome periodic reproductive failure in several ways. (1) Tadpoles grow to a large size at transformation, shortening time at maturity which is size dependent; (2) postmetamorphic growth is very rapid; (3) sexual maturity is attained in 1–2 years by males and 2–3 years by females; (4) males, which suffer higher mortality than females, breed with as many as 3–4 females (personal observation); (5) males and females breed annually; and (6) eggs are laid in a fashion which promotes the most rapid embryonic development possible (Licht 1971), thus reducing time to hatching and subsequent growth. All these adaptations are beneficial to individuals and selected for at the individual level, and in total, reduce chances of population extinction.

In papers on postmetamorphic growth (Turner 1960b) and anuran demography, Turner (1962)

made some very interesting points pertinent to the findings in this paper. He suggested that it is crucial to look at anuran populations as the units to study, especially regarding conspecific populations existing in habitats very different with respect to temperature totals and growing season. He predicted differences in growth rate to be reflected in variation in maximal size, the lengths of prereproductive life span, and probably difference in longevity. The findings on *R. pretiosa* growth reported in this paper may be a consequence of environmental differences and perhaps only by coincidence tend to fit components of the theory proposed by Tilley (1973). Nonetheless, Turner's insights and speculations have been corroborated and it is evident from the comparative data presented that statements on a species' evolutionary or life history strategy must be made tentatively until the species is studied throughout its range, or at least in its most divergent habitats.

COLE, L. E. 1954. The population consequences of life history phenomena. *Q. Rev. Biol.* **29**: 103–137.

EHRlich, P. R., and P. H. RAVEN. 1969. Differentiation of populations. *Science (Wash. D.C.)*, **165**: 1228–1232.

GADGIL, M., and W. H. BOSSERT. 1970. Life historical consequences of natural selection. *Am. Nat.* **104**: 1–24.

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

———. 1971. Breeding habits and embryonic thermal requirements of the frogs, *Rana aurora aurora* and *Rana pretiosa pretiosa*, in the Pacific northwest. *Ecology*, **52**: 116–124.

———. 1974. Survival of embryos, tadpoles, and adults of the frogs *Rana aurora aurora* and *Rana pretiosa pretiosa* sympatric in southwestern British Columbia. *Can. J. Zool.* **52**: 613–627.

PEARL, R., and J. R. MINER. 1935. Experimental studies on the duration of life. XIV. The comparative mortality of certain lower organisms. *Q. Rev. Biol.* **10**: 60–79.

PETTUS, D., and G. M. ANGLETON. 1967. Comparative reproductive biology of montane and piedmont chorus frogs. *Evolution*, **21**: 500–507.

RUIBAL, R. 1955. A study of altitudinal races in *Rana pipiens*. *Evolution*, **9**: 322–338.

TILLEY, S. G. 1973. Life histories and natural selection in populations of the salamander *Desmognathus ochrophaeus*. *Ecology*, **54**: 3–17.

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

———. 1960a. Population structure and dynamics of the western spotted frog, *Rana p. pretiosa* Baird & Girard, in Yellowstone Park, Wyoming. *Ecol. Monogr.* **30**: 251–278.

———. 1960b. Post metamorphic growth in anurans. *Am. Midl. Nat.* **64**: 327–338.

———. 1962. The demography of frogs and toads. *Q. Rev. Biol.* **37**: 303–314.