Age and Size of Wood Frogs, *Rana sylvatica*, from Kuujjuarapik, Northern Quebec

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Length and age of 53 Wood Frogs, *Rana sylvatica*, from Kuujjuarapik in northern Quebec (55°17'N) were compared with similar data from populations in more southern latitudes. Age was estimated by skeletochronology. Mean snout-urostyle length and age were 47.1 mm and 6.1 years in adult males (n = 41) and 50.9 mm and 7.7 years in adult females (n = 8). There was no significant correlation between age and size. The youngest mature males and females were 4 and 6 years old respectively. Mean physiological longevity (mean age in years multiplied by annual number of frost-free days) was 397 days for males and 504 days for females. Comparisons with other populations suggest that sexual dimorphism in size, age, and longevity are species characteristics. Size and age increase with latitude in lowland populations. Physiological longevity is positively related to body size in males from lowland and upland populations. The data do not support the hypothesis that maturity at an early age in males curtails their potential life span. They are consistent with the prediction of longer life span at lower ambient temperatures. In female Wood Frogs, physiological longevity does not follow geographical variation in adult body size.

Key Words: Wood Frog, *Rana sylvatica*, age, growth, longevity, skeletochronology, Kuujjuarapik, Quebec.

The geographic range of the Wood Frog (*Rana sylvatica*) is one of the most extensive among North American ranids. It covers the eastern United States in the favorable forested habitats of the Appalachian and Ozark Mountains, the states of New England, almost all the eastern Canadian provinces including Labrador, the northern two-thirds of Saskachewan, Alberta and British Columbia, and part of the Northwest Territories, Yukon and Alaska (Cook 1984; Conant and Collins 1991) (Figure 1). This cold-adapted species even occurs within the Arctic Circle (up to 69°N); its northern distribution generally follows the northern tree limit.

Such wide distributions in anurans give opportunities for investigation of geographic variations in phenotypical traits such as pigmentation pattern, body proportions, or body size (Ruibal 1957; Martof and Humphries 1959; Pace 1974; Schueler 1982). A general tendency of the Wood Frog for decreasing adult body size with increasing latitudes was established by Martof and Humphries (1959) who, accordingly, concluded that the average body size was a direct consequence of the climate or, more accurately, of the duration and quality of the activity season. Some reverse tendencies in specific regions of north America (Michigan Wood Frogs with smaller than predicted body size, for instance) were tentatively related to historic recolonizations after the Wisconsin glaciation (Martof and Humphries 1959).

Geographic variations in body size of poikilotherms have been repetitively studied in causal relation with ambient temperature (Ray 1960; Atkinson 1994). However, latitudinal and altitudinal trends in anuran body size differ among and within species, perhaps because of demographic strategies (Berven 1982; Hemelaar 1988; Leclair and Laurin 1996). Berven (1982) has suggested for instance, that female Wood Frogs from highland Virginia reach large size due to selection for the production of large eggs in a cold environment. Leclair and Laurin (1996) had related the larger size of northern *R. septentrionalis* to delay in maturity, higher growth rate, and greater mean ages, in comparison with more southern populations.

Most of the demographic data for the adult Wood Frogs come from the extensive studies of Berven (1981, 1982, 1988, 1990), who made use of capture-recapture methods, and from the works of Bastien and Leclair (1992) and Sagor et al. (1998), who estimated age by means of skeletochronology. Bastien and Leclair (1992), using pooled demographic data from Berven (1982), computed mean body size, mean age, and physiological longevity (mean age in years $\times$ number of frost-free days per year) for resident Wood Frogs from lowland Maryland and upland Virginia, and compared the data with those from a Wood Frog population at Trois-Rivières (Quebec). These studies revealed that, in males as in

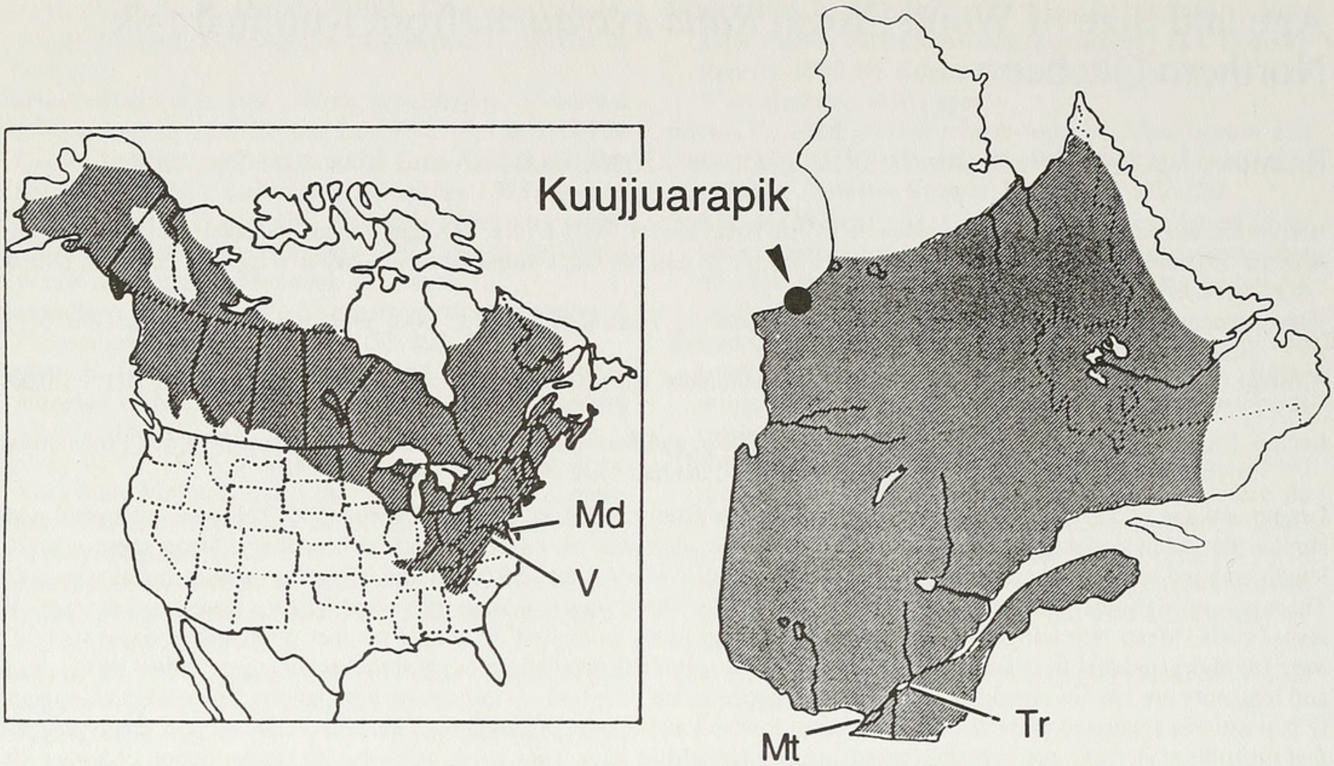

FIGURE 1. General distribution of the wood frog, *Rana sylvatica*, in North America (Md = Maryland V = Vermont) and localization of the study area (Kuujjuarapik) in Quebec Province (Mt = Montreal, Tr = Trois Rivières).

females, both size and age increased from lowland Maryland to Trois-Rivières to upland Virginia. It was also concluded from these studies that physiological longevity in females was stable in the various populations, although body size, mean age, and age at maturity, varied. In males, however, because physiological longevity decreased when mean age deacresed, Bastien and Leclair (1992) suggested that early maturity in male Wood Frogs might curtail the length of their potential life span. Data on size and age of Wood Frogs from Ste-Anne-de-Bellevue on Montreal Island (145 km south of Trois-Rivières) furnished by Sagor et al. (1998) fit perfectly with these geographic trends; physiological longevity was not computed, however.

Many of the body size tendencies of Wood Frogs established by Martof and Humphries (1959) rest on a limited number of museum specimens (14 for all of Quebec; only one specimen from Great Whale River). Moreover, age has infrequently been determined in Wood Frog demographic studies, although body size of breeding adults is a widely measured variable. It is therefore worthwhile to study additional populations of *R. sylvatica* in order to better relate geographic variations in age/size relationships to environmental conditions.

The present work addresses whether a population of Wood Frogs (a sample of 41 adult males and 8 adult females) from Kuujjuarapik, northern Quebec, supports or contradicts the geographic trends in size, age, and physiological longevity found for Wood Frogs from the study of a few populations where age could be determined (Berven 1982; Bastien and Leclair 1992; Sagor et al. 1998). Owing to cold ambient temperatures and the very short growing season in Kuujjuarapik, we expected older and larger Wood Frogs here than anywhere south of this locality. We also asked: Does physiological longevity remain stable among female populations of Wood Frogs? and Does this parameter continue to vary with age in males?

Material and Methods

Kuujjuarapik (Poste-de-la Baleine) is situated on the east shore of Hudson Bay at the mouth of the Great Whale River (55°17′N, 77°45′W) (Figure 1). The study site, on the northeastern limit of the village, is 1.3 km from the Hudson Bay coast and encompasses one main pond (50 m in diameter, 1 m depth) that overflowed into four secondary ponds (10 m in diameter, less than 10 cm depth). These ponds were fed by snow melt. There are an average of 65 frost-free days per year in the region (Wilson 1971). Breeding Wood Frogs were caught by hand or dipnet in ponds, during the day or at night, between 8 June and 8 July 1991. Air and water temperatures on 11 June at 1500h were 8 and 10°C respectively. The frogs were sexed (males with strong forearms and nuptial thumb pads), measured to nearest mm (SUL: snout-urostyle length), their longest (fourth) hind digit amputated at the level of articulation between the first and second proximal phalanges (for age estimation by skeletochronology), and released alive at the site of capture.

The age of frogs was estimated by the spatial distribution of the lines of arrested growth (LAG) in cross-sectioned phalanges, taking into account endosteal resorption that can destroy the most inner LAGs (Leclair 1990; Bastien and Leclair 1992). The phalanges were hand-cleaned, decalcified in 3% nitric acid, and cut into 16 µm thick sections with a freezing microtome. Sections were stained with Ehrlich hematoxylin and mounted on glass slides in glycerin. The age of each animal was independently estimated by the first three authors. The estimates of ages never diverged more than one year between the three interpretations. Divergences were mostly due to difficulties in separating the more closely packed peripheral LAGs in the oldest animals. Partial resorption of the first LAG occurred in 27% and complete resorption in 35% of the animals. No known-aged individuals were available. The analysis rests on the premise that LAGs in this population of *R. sylvatica* are annual formations as has been experimentally demonstrated in other cold temperate ranid frogs (Smirina 1972; Francillon and Castanet 1985).

The sample size of females was too low to attempt statistical intersex comparisons. However, we used linear regressions to test the relationships between age and size in both sexes. Statistics were generated with the StatView Students program.

Results and Discussion

Adult female body size (SUL) ranged from 47 to 54 mm (mean: 50.9 mm) whereas adult male body size ranged from 41 to 50 mm (mean: 47.1 mm) (Figure 2). A sexual size dimorphism in favour of females was also encountered in other populations of Wood Frog (Cook 1967; Berven 1982; Gilhen 1984; Davis and Folkerts 1986; Bastien and Leclair 1992; Sagor et al. 1998) and in the museum specimens examined by Martof and Humphries (1959).

The mean age of adult female Wood Frogs from Kuujjuarapik was 7.7 years (range: 6–10 years) whereas that of adult males was 6.1 years (range: 4–8 years; Figure 3). Female Wood Frogs from Maryland-Virginia (Berven 1982) and from more southern Quebec (Bastien and Leclair 1992; Sagor et al. 1998) also averaged older than males. However, there was no correlation between body size and age in the study population ($r = 0.058$ in males, $r = 0.59$ in females; $p > 0.05$ in both cases). The correlation between age and size is generally low in amphibians (Halliday and Verrell 1988) although it was significant in both sexes in the Wood Frog population of Trois-Rivières (Bastien and Leclair 1992). Higher longevity after the attainment of adult body size (Table 1) and strong year-to-year variations in growth performance of Wood Frogs in northern conditions may explain the loss of correlation between size and age at Kuujjuarapik. Similarly, Hemelaar (1988) found that *Bufo bufo* lacks such correlation between age and size in some populations characterized by older individuals but not in others with smaller and younger specimens.

The onset of maturity is generally correlated with an abrupt decline in the rate of somatic growth in anurans due to an energy drift from growth to repro-

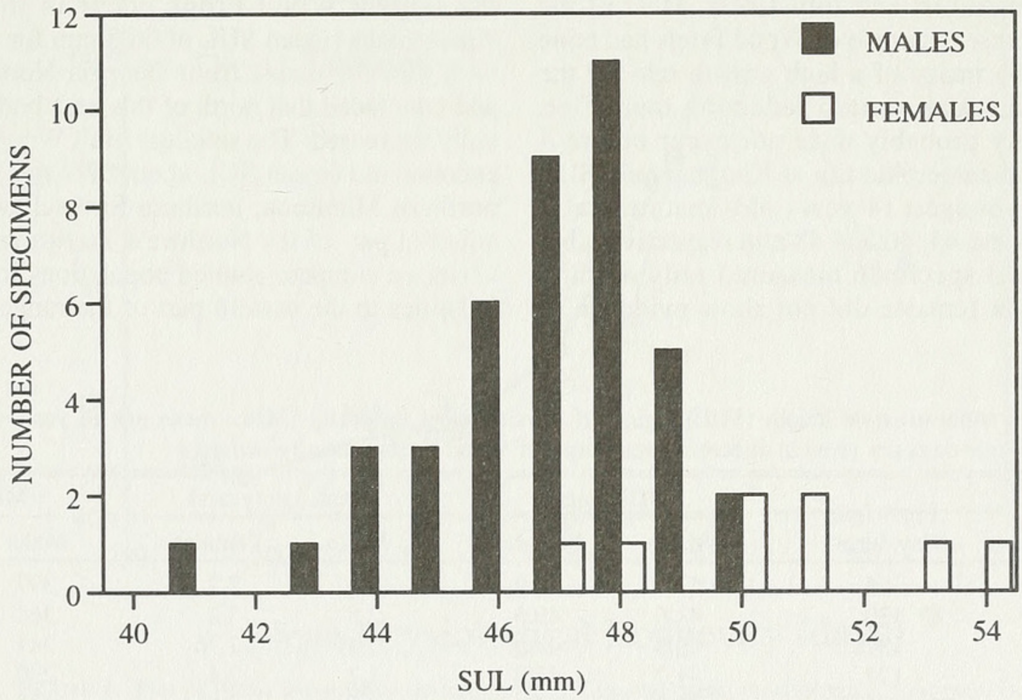

FIGURE 2. Body size (SUL: snout-urostyle length) distribution of adult *Rana sylvatica* from Kuujjuarapik.

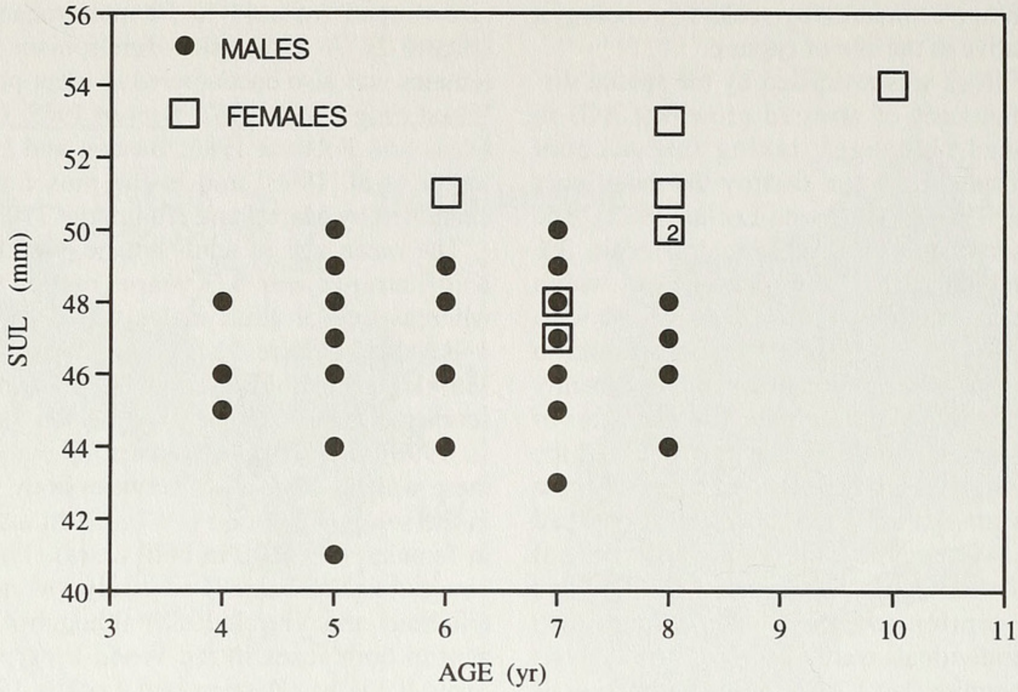

FIGURE 3. Relationships between body size (SUL: snout-urostyle length) and age in *Rana sylvatica* from Kuujjuarapik. The number in one female block indicates a double observation; many male observations are in superposition for ages 5 to 7.

duction (Ryser 1989; Jørgensen 1986). This decline in growth influences the spatial arrangement of LAGs in bone cortex. Kleinenberg and Smirina (1969) and Gibbons and McCarty (1983) have observed for *R. temporaria* and *Bufo bufo* that the onset of sexual maturity was related to a sudden rapproachment of LAGs. In many instances this osteological criterion was used to assess the age at maturity in amphibians (Barbault et al. 1979; Caetano et al. 1985; but see Augert and Joly 1993). Most of the males in the present sample of Wood Frogs had bone cortex with the image of a high growth rate for the first four years and a sharp reduction thereafter. Thus, maturity probably does not occur before 4 years of postmetamorphic life at Kuujjuarapik. SUL of the three youngest (4 years old) mature males encountered were 45, 46 and 48 mm respectively but one 5 year-old specimen measured only 41 mm. Bone cortex in females did not show evidence of LAG rapproachment. The youngest mature female however was 6 years old (51 mm), thus, it may be postulated that females delay reproduction relative to males and continue to grow at a high rate for an additional two years. Size at metamorphosis is unknown for the study population and, in the absence of a correlation between age and size, growth rates could not be calculated.

Martof and Humphries (1959) had determined that the largest Wood Frogs occur in the southern Apalachians (mean SUL of 66.8 mm for females and 54.8 mm for males from Georgia-North Carolina) and concluded that north of this area body size gradually decreased. The smallest adult Wood Frogs they encountered (mean SUL about 37.7 mm) came from northern Manitoba, northern Saskachewan and the adjacent part of the Northwest Territories. However, when we compare studied populations from lowland localities in the eastern part of the range (Maryland,

TABLE 1. Mean snout-urostyle length (SUL), age, and physiological longevity (MPL: mean age in years multiplied by number of frost-free days per year) in different populations of Wood Frogs, *Rana sylvatica*.

Population	Frost-free days/year	SUL (mm)		Mean age (years)		MPL (days)	
		Males	Females	Males	Females	Males	Females
Kuujjuarapik	65	47.1	50.9	6.1	7.7	397	504
Trois-Rivières[a]	130	43.6	49.6	2.8	3.2	364	416
Montreal[b]	137	43.6	48.8	2.49	2.76	341	378
Maryland[c]	177	41.7	47.7	1.7	2.4	290	421
Virginia[c]	121	55.3	64.4	3.6	3.8	438	458

[a]From Bastien and Leclair (1992); [b]Sagor et al. (1998); [c]Berven (1982)

Montreal, Trois-Rivières, Kuujjuarapik), we observe an *increase* in body size of Wood Frogs with increasing latitudes (Table 1); the phenomenon is more evident in males. An European vicariante species, *R. temporaria*, is also known to increase in size with both latitudes and altitudes (Miaud and Guyétant 1998). The increase in body size in *R. sylvatica* is accompaned by a more than three-fold increase in mean age (calendar years; Table 1). Although smaller, specimens from Kuujjuarapik are twice as old as those of upland Virginia. Our results are thus consistent with the general observation that for ectotherms longer life spans are favored at low temperatures (review in Sohal 1976; Caetano and Castanet 1993; Ryser 1996).

Differences in age are tempered when this parameter is expressed as mean physiological longevity (Table 1). Male Wood Frogs from Kuujjuarapik show a lower physiological longevity (397 days) than males from Virginia (438 days). We can observe that geographic differences in Wood Frog body size, at least in males, are closely related to physiological longevity (Figure 4). However, with the assumption of sexual maturity at 4 years in males from Kuujjuarapik, we were expecting a much higher longevity for these animals. This last result contradicts the Bastien and Leclair (1992) hypothesis of a negative trade-off between early age at maturity and physiological longevity. Yet, with a maturity at 4 years and a mean age of 6 years, most of the male Wood Frogs in Kuujjuarapik could participate at least in three reproductive seasons. Much longer reproductive lifespan may not be selected for. Berven (1990) estimated that 84% of the male and 86.8% of the female Wood Frogs in Maryland contribute to only one reproductive season. A similar increase in iteroparity with latitudes and altitudes in *R. temporaria* is viewed as a compensation for lower fecundity (Miaud and Guyétant 1998).

Among the lowland populations, female Wood Frogs from Kuujjuarapik have the highest physiological longevity (504 days) and the largest body size, but they stay definitely smaller than their conspecifics from upland Virginia (Table 1). Physiological longevity then does not explain geographical variation in female Wood Frog body size (Figure 4).

When decreasing temperatures reduce growth rate in ectotherms, models predict that larger adult body sizes are produced (Atkinson 1994). Our results seem consistent with this prediction although we do not have direct observation on Wood Frog growth rate at Kuujjuarapik. Comparative demography of *R. sylvatica* has shown that growth rate does not passively follow ambient temperatures but is genetically adapted to specific environmental conditions (Berven 1982). From the data of Berven (1982) on mean size of male Wood Frogs at specific ages, size at transformation, and number of frost-free days, we can conclude that juvenile growth rate is equal (*ca* 0.14 mm/day; Appendix 1) in lowland Maryland and upland Virginia, although mean temperatures are

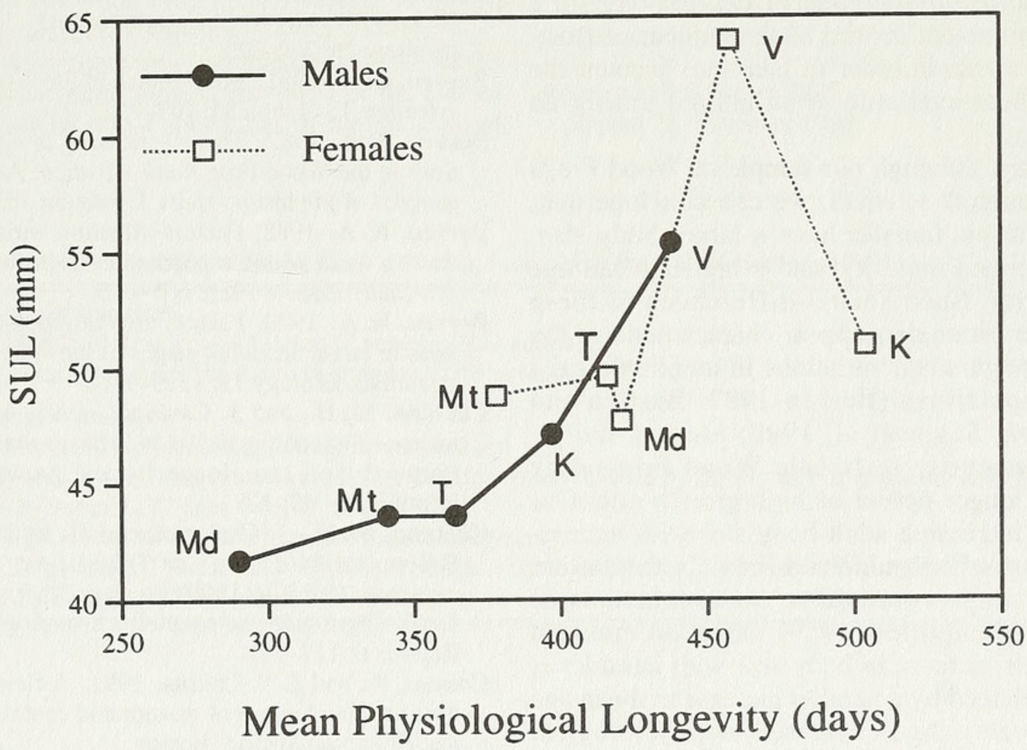

FIGURE 4. Plot of mean snout-urostyle length (SUL) against mean physiological longevity in adult Wood Frogs from different populations. K: Kuujjuarapik, Md: Maryland, Mt: Montreal, T: Trois-Rivières, V: Virginia (see Table 1 for references).

5°C lower in the uplands. Thus, growth rate appears to compensate for differences in temperature in these frogs. A higher per day growth rate during the active season may characterize Wood Frogs from northern or cold localities.

Such compensation phenomena are more frequently observed in anuran *embryonic* development where the physiological processes of growth appear temperature-adapted (review in Rome et al. 1992). In transformed animals, the compensation may have a physiological and/or behavioral components. Martof and Humphries (1959) found, for example, that Wood Frogs from Alaska-Yukon area were gorged with food, their stomachs usually distended due to their extensive feeding. Mink Frogs (*R. septentrionalis*) from northern latitudes were also found to have greater stomach contents, a higher per day growth rate, and larger body size compared to Mink Frogs from more southern regions (Leclair and Laurin 1996).

Although growth rate may be compensated, or even meliorated in cold environments, the growing season may be so short that more time (in years) is required to reach an appropriate reproductive size. Female Wood Frogs from Kuujjuarapik apparently require six calendar years to reach a minimum reproductive size. Any reproductive advantages of larger size (such as increased fecundity or larger eggs) may be constrainted by the likelihood of survival to the next breeding period (Pace 1974). Nevertheless, females with the highest physiological longevity from Kuujjuarapik should have reached the largest body size. Perhaps to quantify physiological longevity we should use the number of degrees-days in a specific environment instead of the number of frost-free days per year in order to take into account the amount of heat available to an animal during an active season.

In summary, although our sample of Wood Frogs from Kuujjuarapik is small, we can conclude that, relative to males, females have a larger body size, longer postponed maturity, and a higher mean age and longevity. Such sexual differences in these demographic parameters appear characteristic of the species although some variations in amplitude exist between populations (Berven 1982; Bastien and Leclair 1992; Sagor et al. 1998; present study). Postponed maturity in female Wood Frogs may allow for a longer period of high growth rate. Our result of an increasing adult body size with increasing latitudes for lowland Wood Frogs in the eastern part of the range contradicts the conclusions of Martof and Humphries (1959) based on museum material. This increase in body size with latitudes is partially explained by a parallel increase in mean age (calendar years). Age expressed as physiological longevity can also explain larger sizes in upland male populations; it does not appear related to age at sexual maturity, however, contrary to an earlier hypothesis. Physiological longevity is also variable among female populations but does not show any obvious relation with mean adult body size.

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Literature Cited

Atkinson, D. 1994. Temperature and organism size — a biological law for ectotherms? Advances in Ecological Research 25: 1–58.

Augert, D., and **P. Joly.** 1993. Plasticity of age at maturity between two neighbouring populations of the common frog (*Rana temporaria* L.). Canadian Journal of Zoology 71: 26–33.

Barbault, R., J. Castanet, H. Francillon, and **A. de Ricqlès.** 1979. Détermination de l'âge chez un anoure déserticole *Bufo pentoni*, Anderson 1893. Terre et Vie, Revue d' Ecologie 33: 129–141.

Bastien, H., and **R. Leclair.** 1992. Aging Wood Frogs (*Rana sylvatica*) by skeletochronology. Journal of Herpetology 26: 222–225.

Berven, K. A. 1981. Mate choice in the Wood Frog, *Rana sylvatica*. Evolution 35: 707–722.

Berven, K. A. 1982. The genetic basis of altitudinal variations in the Wood Frog *Rana sylvatica*. An experimental analysis of life history traits. Evolution 36: 962–983.

Berven, K. A. 1988. Factors affecting variation in reproductive traits within a population of Wood Frogs (*Rana sylvatica*). Copeia 1988: 605–615.

Berven, K. A. 1990. Factors affecting population fluctuations in larval and adult stages of the Wood Frogs (*Rana sylvatica*). Ecology 71: 1599–1608.

Caetano, M. H., and **J. Castanet.** 1993. Variability and microevolutionary patterns in *Triturus marmoratus* from Portugal: age, size, longevity and growth. Amphibia-Reptilia 14: 117–129.

Caetano, M. H., J. Castanet, and **H. Francillon.** 1985. Détermination de l'âge de *Triturus marmoratus marmoratus* (Latreille 1800) du Parc National de Peneda Gerês (Portugal) par squelettochronologie. Amphibia-Reptilia 6: 117–132.

Conant, R., and **J. T. Collins.** 1991. A field guide to reptiles and amphibians of eastern and central North America. Houghton Mifflin, Boston.

Cook, F. R. 1967. A analysis of the Herpetofauna of Prince Edward Island. National Museum of Canada Bulletin 212: 1–60.

Cook, F. R. 1984. Introduction aux amphibiens et reptiles du Canada. Musées Nationaux du Canada, Ottawa.

Davis, M. S., and **G. W. Folkerts.** 1986. Life history of the Wood Frog, *Rana sylvatica* LeConte (Amphibia: Ranidae), in Alabama. Brimleyana 12: 29–50.

Francillon, H., and **J. Castanet.** 1985. Mise en évidence expérimentale du caractère annuel des lignes d'arrêt de croissance squelettique chez *Rana esculenta* (Amphibia, Anura). Comptes-rendus de l'Académie des Sciences de Paris 300: 327–332.

Gibbons, M. M., and **T. K. McCarty.** 1983. Age determination of frogs and toads (Amphibia, Anura) from north-western Europe. Zoologica Scripta 12: 145–151.

Gilhen, J. 1984. The amphibians and reptiles of Nova Scotia. Nova Scotia Museum, Halifax.

Halliday, T. R., and **P. A. Verrell.** 1988. Body size and age in amphibians and reptiles. Journal of Herpetology 22: 253–265.

Hemelaar, A. 1988. Age, growth and other population characteristics of *Bufo bufo* from different latitudes and altitudes. Journal of Herpetology 22: 369–388.

Jørgensen, C. B. 1986. External and internal control of patterns of feeding, growth, and gonadal function of a temperate zone anuran, the toad *Bufo bufo*. Journal of Zoology (London) 210: 211–241.

Kleinenberg, S. E., and **E. M. Smirina.** 1969. A method for age determination in amphibians [in Russian]. Zoological Zhurnal 48: 1090–1094.

Leclair, R. 1990. Relationships between relative mass of the skeleton, endosteal resorption, habitat and precision of age determination in ranid amphibians. Annales des Sciences Naturelles, Zoologie, Paris 11: 205–208.

Leclair, R., and **G. Laurin.** 1996. Growth and body size in populations of mink frogs *Rana septentrionalis* from two latitudes. Ecography 19: 296–304.

Martof, B., and **R. L. Humphries.** 1959. Geographic variation in the Wood Frog *Rana sylvatica*. American Midland Naturalist 61: 350–389.

Pace, A. E. 1974. Systematic and biological studies of the leopard frogs (*Rana pipiens* complex) of the United States. Miscellaneous Publications of the Museum of Zoology, University of Michigan, Ann Arbor, number 148.

Miaud, C., and **R. Guyétant.** 1998. Plasticité et sélection sur les traits de vie d'un organisme à cycle complexe, la grenouille rousse *Rana temporaria* (Amphibien: Anoure). Bulletin de la Société Zoologique de France 123: 325–344.

Ray, C. R. 1960. The application of Bergman's and Allen's rules to the poikilotherms. Journal of Morphology 106: 85–108.

Rome, L. C., E. D. Stevens, and **H. B. John-Alder.** 1992. The influence of temperature and thermal acclimation on physiological function. Pages 183–205 *in* Environmental physiology of the amphibians. *Edited by* M. E. Feder and W. W. Burggren. The University of Chicago Press, Chicago.

Ruibal, R. 1957. An altitudinal and latitudinal cline in *Rana pipiens*. Copeia 1957: 212–221.

Ryser, J. 1989. Weight loss, reproductive output, and the cost of reproduction in the common frog, *Rana temporaria*. Oecologia 78: 264–268.

Ryser, J. 1996. Comparative life histories of low- and high-elevation populations of the common frog *Rana temporaria*. Amphibia-Reptilia 17: 183–195.

Sagor, E. S., M. Ouellet, E. Barten, and **D. M. Green.** 1998. Skeletochronology and geographic variation in age structure in Wood Frog, *Rana sylvatica*. Journal of Herpetology 32: 469–474.

Sohal, R. S. 1976. Metabolic rate and lifespan. Interdisciplinary Topics in Gerontology 9: 25–40.

Schueler, F. W. 1982. Geographic variation in skin pigmentation and dermal glands in the northern leopard frog, *Rana pipiens*. Publication in Zoology of the National Museum of Natural Sciences 16.

Smirina, E. M. 1972. Annual layers in bones of *Rana temporaria*. Zoological Zhurnal 51: 1529–1534.

Wilson, C. V. 1971. Le climat du Quebec (1ère partie): Atlas climatique. Service météorologique du Canada, Etudes climatiques II.

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APPENDIX 1. Growth rate of Wood Frogs, *Rana sylvatica*, based from the data of Berven (1982).

Body size at transformation
— Lowland Maryland Residents: 14.9 mm (3 samples, 221 animals)
— Upland Virginia Residents: 18.6 mm (4 samples, 1049 animals)

Male juvenile growth rate
— Lowland Maryland Residents (most frogs are mature at 1 year):
mean body size at age 1 less mean body size at transformation divided by the number of frost-free days per year, or (40.2 mm-14.9 mm) / 177 days = 0.143 mm/day
— Upland Virginia Residents (most frogs are mature at 2 years):
mean body size at age 2 less mean body size at transformation divided by the number of frost-free days per year, or (54.7 mm-18.6 mm) / (2 × 121 days) = 0.149 mm/day