2000

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Demographic (snout–vent length, skeletochronologically estimated age) and reproductive (fecundity, ova size) characteristics were examined in *Rana areolata* from Williamson County, Illinois. Fifty-nine frogs (36 males, 23 females) were sampled from breeding choruses in March 1996. Hematoxylinophilic annular lines of arrested growth (LAG) were detected in the diaphyses of cross-sectioned phalanges of all sampled frogs. t-tests revealed that male age (mean = 3.53 yr) and female age (mean = 3.83 yr) were not significantly different, but male SVL (mean = 82.78 mm) was significantly smaller than that of females (mean = 89.61 mm). There were positive correlations between SVL and age for both males ($r^2 = 0.66$) and females ($r^2 = 0.58$), with males maturing earlier than females. Eggs from 15 clutches (12 ovarian ova complements from dissected females; three clutches oviposited in the lab) were counted, and mean clutch size was 4868 ova. There were positive correlations between female SVL and clutch size ($r^2 = 0.76$) and between female age and clutch size ($r^2 = 0.41$). Mean ovum/embryo diameter for all yolked ovarian complements, and two oviposited clutches (preserved at the blastula stage or earlier), was 2.05 mm. Clutch size was inversely correlated ($r^2 = -0.46$) with mean ovum size.

INDEX DESCRIPTORS: age; demography; population biology; fecundity; ovum size; *Rana areolata*, skeletochronology, Southern Illinois.

The crayfish frog, *Rana areolata*, occurs in the southern and central United States, including portions of the midwestern and Great Plains States of Illinois, Indiana, Iowa, Kansas, and Missouri (Altig and Lohoefener 1983, Conant and Collins 1991). Much of this species' range in these states was formerly covered in tallgrass prairie, most of which was converted to row-crop agriculture after European settlement, and it is believed that habitat loss has contributed to population declines in several of these states (Busby and Brecheisen 1997, Johnson 1987). *Rana areolata* is now listed as an endangered species in Iowa (Christiansen and Baily 1991) and Indiana (Simon et al. 1992), and considered a species of special concern in Missouri (Johnson 1987) and Kansas (Busby and Brecheisen 1997, Collins 1993). In Illinois, *R. areolata* is documented from the southern third of the state (Smith 1961), where it still occurs in localized populations (M. Redmer pers. obs. 1991–97).

Little is known about demography and longevity of amphibians (Duellman and Trueb 1986), even of "common" species. Such data could be particularly useful in devising conservation strategies for uncommon species such as *Rana areolata*. There have been few studies on the reproductive and population biology of *R. areolata* (Busby and Brecheison 1997, Parris and Semlitsch 1998). Bragg (1953) and Smith et al. (1948) reported on breeding season, clutch and ovum/embryo sizes, and snout-vent lengths (SVL) of samples from Oklahoma and Illinois, respectively. Busby and Breicheisen (1997) reported on chorusing phenology and habitat of *R. areolata* in Kansas. Halliday and Verrell (1988) found two techniques to be reliable for estimating age in amphibians and reptiles: capture-mark-recapture, and skeletochronology. Skeletochronology involves visualizing and counting annular lines of arrested growth (LAGs; each representing the end of one year of growth) located between bone growth areas from cross-sectioned diaphyses of long bones such as femora

or phalanges (Castanet and Smirina 1990, Halliday and Verrell 1988). Skeletochronology is an appropriate method for estimating age in amphibians and reptiles from populations occurring in seasonal climates (Halliday and Verrell 1988). When phalanges are used, skeletochronology is an effective non-lethal technique for estimating age of individual amphibians, and it has become a particularly popular technique within the past 20 years (Bastien and LeClair 1992).

Reproductive output and larval survivorship are important regulators of amphibian population cycles (Berven 1990, Semlitsch et al. 1996). Most studies of anuran fecundity and size have shown negative correlations between clutch and ovum sizes, and positive correlations between female body size and clutch parameters (Duellman and Trueb 1986, Salthe and Duellman 1973, Salthe and Mecham 1974). Few studies have demonstrated age correlations with clutch parameters, though some studies have shown positive age-body size correlations (Duellman and Trueb 1986, but see Halliday and Verrell 1988), and age also could have corresponding correlations with reproductive characteristics such as clutch size, ovum size, etc.

Because of recent concern over the worldwide decline of populations of some amphibian species (Blaustein 1994, Blaustein and Wake 1995, Wake 1991), baseline data on the natural history of most species are needed, and development of protocols for monitoring and comparing trends in basic population characteristics are imperative, especially for rare species. In this study, I used skeletochronology to estimate age in a population of *R. areolata* from southern Illinois. I examined correlations between: (A) age and SVL, (B) age and clutch size, (C) SVL and clutch size, and (D) clutch size and mean ovum size. The value of these correlations to conservation of anurans in general, and in planning further population studies of *R. areolata* are discussed.

METHODS

Material and Study Site

Fifty-nine *Rana areolata* (36 males, 23 females) were collected by hand or with a dipnet at or around three ephemeral or semi-permanent breeding ponds on 14–17 or 24–25 March 1996. Five individuals (two males, three females) were collected alive on roads adjacent to the ponds. The study site was located in extreme western Williamson County, Illinois, near Crab Orchard National Wildlife Refuge (37° 42'N, 89° 07'W). The ponds are close enough to each other that choruses at one pond could be heard from the others, and thus the frogs sampled for this study are considered part of the same population. The soil in the study area was primarily clay and supported a high water table. Large burrowing crayfishes (especially *Cambarus diogenes*, *Fallicambarus fodiens*) and their conspicuous chimneys were abundant in the study area, and probably provided retreats for *R. areolata*. Land use in the surrounding area was primarily agricultural (hay fields, row crops, and/or pastures), with some shrubby fields and residential housing.

Sampling Protocol

After capture, individual frogs were placed in plastic coolers or buckets for transport to the laboratory, where sex and SVL (to the nearest mm) were recorded. From each frog the fourth (long) toe was amputated below the proximal joint of the penultimate and third phalanges. Toes were fixed in individually labeled vials of 10% formalin for a minimum of 24 h, rinsed for 12 h in running tap water, and stored in individually labeled vials of 70% ethanol. Most frogs were returned to the original pond < 12 h of capture, but 14 females were euthanized and preserved to obtain reproductive information.

Reproductive Data

Preserved females were dissected, and ovarian (whole yolked follicles) ova were removed and counted manually. Subsamples of ten ova per clutch were measured to the nearest 0.05 mm with a dissecting microscope and a calibrated ocular micrometer. Because most ova were non-spherical, widest X and Y axes were measured, added, and then divided by two to determine average diameter. To determine if females oviposited their entire clutches, three amplexed pairs were allowed to oviposit in the lab. Females from these pairs, and their eggs, were preserved. The females were larer dissected to determine presence or absence of remaining ova in the oviducts. Most eggs produced in this manner were preserved within 4 hr of oviposition. These were counted, and ten ova from each clutch were removed from their jelly envelopes, and measured in the same fashion as ovarian ova.

Tissue Preparation

Preserved toes were manually defleshed and rhe penultimate phalanx from each was separated from the others. These were decalcified by immersion in Kristensen's formic acid solution for 10 h and rinsed for 24 h in running tap water. Samples were automatically (V.I.P.® Tissue-Tek machine) dehydrated, cleared, and infiltrated with paraffin. Phalanges were embedded individually in small paraffin blocks and cross-sectioned at 10 μm with a microtome. Ten to 30 diaphysial sections of each bone were attached with adhesive gelatin to microscope slides. The samples were hydrated and cleared with a series of alcohol steps, and stained with Shandon® instant regressive hematoxylin for 15 min. Samples were then dehydrated, mounted on glass microscope slides, and were covered with Permount® mounting medium and glass coverslips.
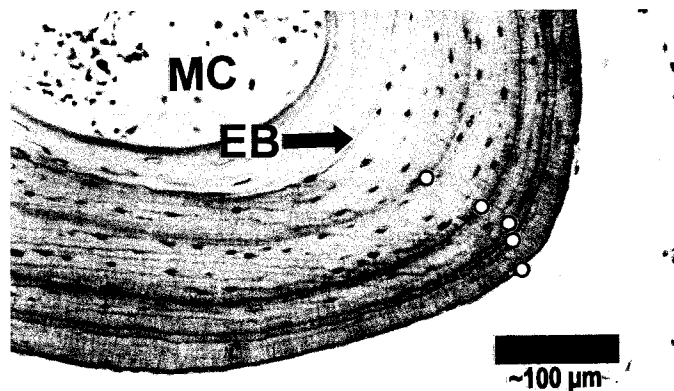

Fig. 1. Photomicrograph of a hematoxylin-stained phalangeal cross-section of a 5-yr-old (100 mm SVL) female *Rana areolata* from a population in Williamson County, Illinois. Key to abbreviations: MC = medullary cavity, EB = limit of endosteal bone, open circles = periosteal lines of arrested growth (LAGs). Magnification = 160×.

Sample Evaluation

Interpretation of LAG followed the procedures and criteria of published studies on the skeletochronological technique (Castanet and Smirina 1990, Smirina 1994). Cross sections were visualized with a binocular microscope. For age estimates, periosteal LAG were visualized and counted, with the outer bone perimeter included as one LAG. Bone resorbtion sometimes causes LAGs in the early year classes to be obscured or obliterated by endosteal bone growth (EB), thus causing age to be underestimated in some individuals (Hemelaar 1985, Sagor et al. 1998). Because I detected bone remodeling in my sample, I used the techniques described by Sagor et al. (1998) to statistically estimate the amount of periosteal bone resorbtion. If metamorphosis lines were present, age was estimated by counting periosteal LAGs (each LAG = 1 yr). Tissues were collected from frogs that had just emerged from hibernation, the LAG deposited during the winter was not discernible from the outer bone perimeter; thus the outer perimeter was counted as a LAG. In some instances, EB was broken or absent (as evidenced by resorbtion patterns in periosteal bone layers), probably because of damage caused by the microtome blade. In these instances, the diameter of the space where MC and EB had been was recorded as the diameter of EB. To determine what percentage of early LAGs may have been obliterated by endosteal bone growth, I compared the mean diameter of endosteal bone with mean diameters of the innermost and second visible LAGs. If the diameter of the endosteal region was ≥ 2 SD more than the group mean, I concluded that LAG 1 had been resorbed, and that the innermost LAG actually was LAG 2. If only part of a LAG was obscured by endosteal bone remodeling, the area of endosteal bone was calculated. If it was > 2 SD smaller than the mean of the next LAG, I interpreted the partial visible LAG as LAG 1.

RESULTS

Hematoxylinophilic LAGs were detected in phalangeal sections of all specimens examined (Fig. 1). The range of LAG diameters overlapped between all age classes (Table 1). Metamorphosis lines were observed in only three (5%) samples. In eight (13.5%) individuals, endosteal bone remodeling was extensive enough that it encroached over periosteal bone and partially obliterated LAG. In each instance, part of the innermost LAG remained, and measured endosteal bone

Table I. Diameters of endosteal bone (EB) and non-remodeled periosteal LAGs of *Rana areolata* from a population in western Williamson County, Illinois.

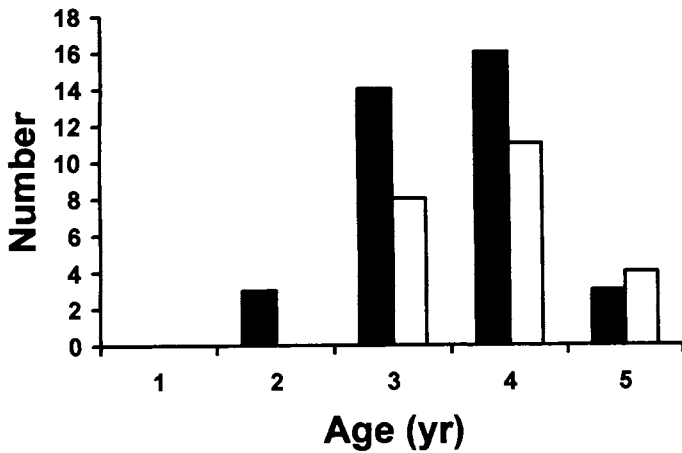| EB/LAG | N | Diameter (μm) | | |
		Mean ± SD	Min	Max
EB	56	373 ± 40.4	315	440
LAG 1	48	489 ± 56.6	400	560
LAG 2	59	608 ± 81.1	485	775
LAG 3	56	669 ± 89.5	500	880
LAG 4	34	714 ± 87.0	575	785
LAG 5	7	835 ± 37.4	785	875

Fig. 2. Skeletochronologically estimated age frequency distributions of *Rana areolata* from Williamson County, Illinois. Males are indicated by shaded bars, females by white bars.
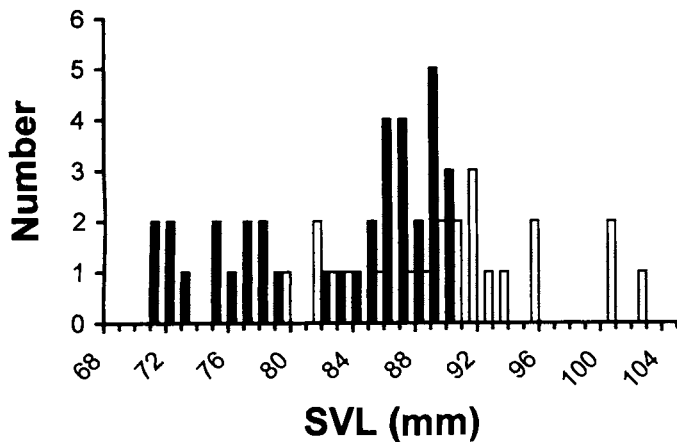

Fig. 3. Length frequency distributions of *Rana areolata* from Williamson County, Illinois. Males are indicated by shaded bars, females by white bars.

diameters < 2 SD greater than the mean of all complete LAG 1 diameters and < 3 SD less than the mean of LAG 2 diameters indicated that the incomplete LAG were LAG 1.

The mean skeletochronologically estimated age of males was 3.53 yr (SE = 0.13, range = 2–5 yr, n = 36; Fig. 2), while that of
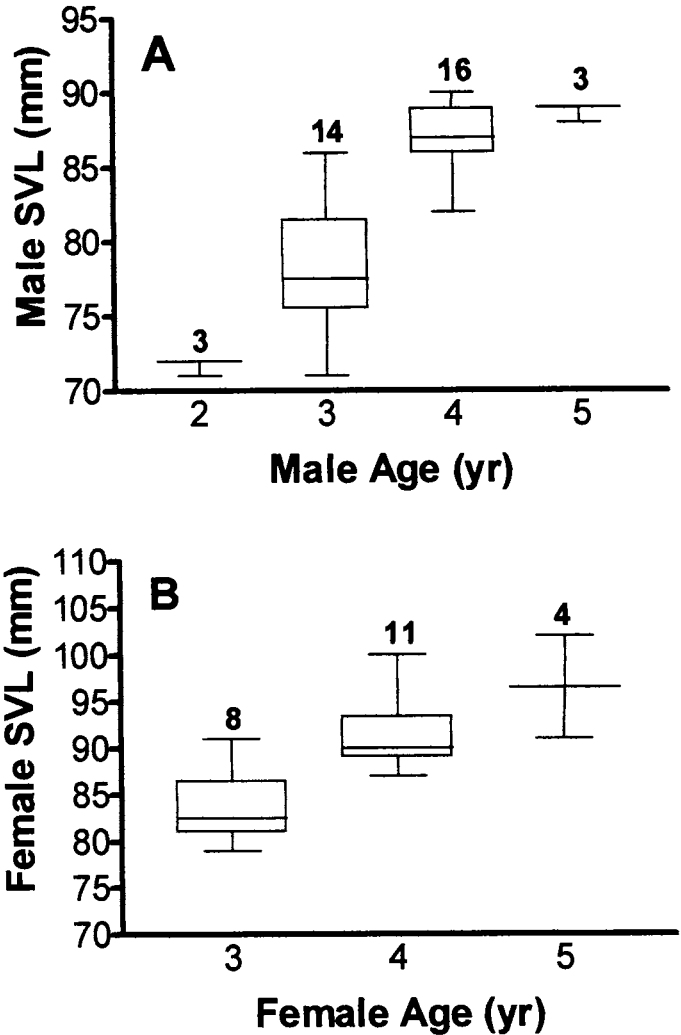

Fig. 4. Age-body length distribution in *Rana areolata* from a population in Williamson County, Illinois. (A) Males, (B) females. Key: Numbers above columns = sample sizes; extreme upper and lower lateral lines = range of data; upper and lower edges of boxes = interquartile values, lines in boxes = mean values.

females was 3.83 yr (SE = 0.15, range = 3–5 yr, n = 23; Fig. 2). Mean SVL of males was 82.78 mm SVL (SE = 1.06; range = 71–90 mm; Fig. 3), while that of females was 89.64 mm SVL (SE = 1.30; range = 79–102 mm; Fig. 3). Age distributions between males and females did not differ significantly (t = 1.49; df = 57; P = 0.14), but size distributions did differ significantly (t = 4.19; df = 57; P < 0.0001). There were strong positive correlations between SVL and age of males (r^2 = 0.66, P < 0.0001) and females (r^2 = 0.58, P < 0.0001), though there was some overlap in size between each sequential age class (Fig. 4A, B).

Fifteen clutches of *R. areolata* ova were sampled, 12 of which consisted of ovarian ova removed from dissected females, and three which consisted of eggs oviposited in the lab by females that were kept in amplexus with mates. Mean clutch size was 4868 ova (SD = 1277; range = 3208–6807). Mean ovum/embryo diameter was determined for all ovarian clutches, and two of the three oviposited clutches preserved at the blastula stage or earlier (2.05 mm; SD = 0.11; range = 1.80–2.20). Ova from one clutch developed past the yolk plug stage, and mean ovum diameter (3.58 mm) from this
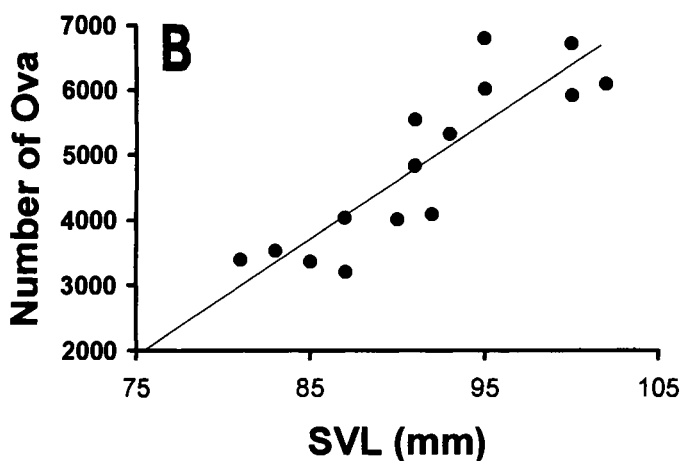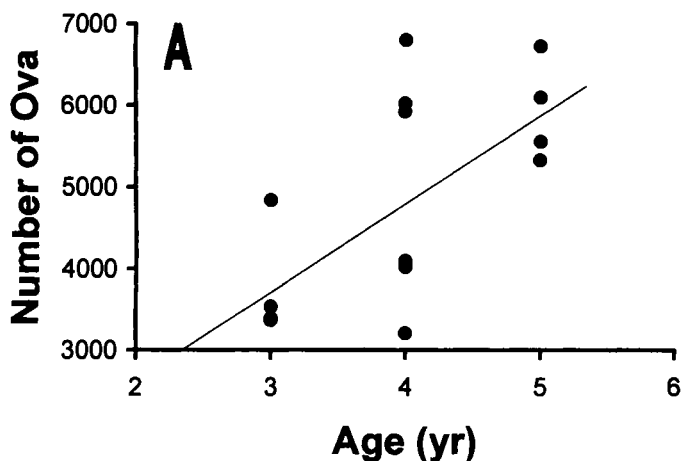
Fig. 5. Relationship between clutch size and: (A) female age, and (B) female SVL in *Rana areolata* from a population in Williamson County, Illinois.
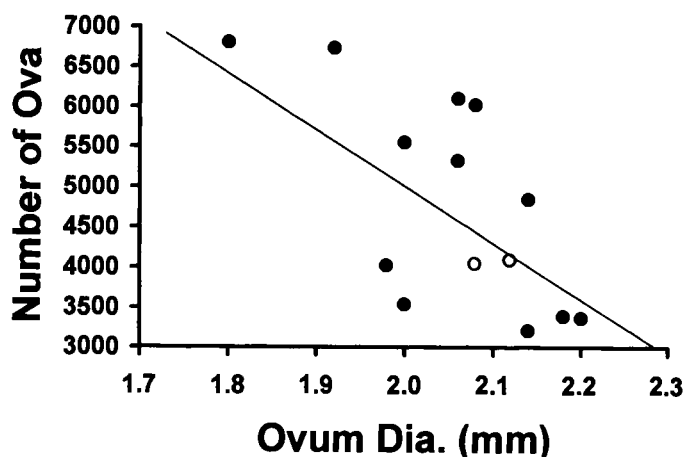

Fig. 6. Relationship between clutch size and mean ovum diameter in oviposited (open circles) and ovarian ova (solid circles) of *Rana areolata* from a population in western Williamson County, Illinois.

clutch was not used in analyses because the size of amphibian embryos increases incrementally during development, and may be > 10% larger than non-cleaved ova by the time gastrulation begins (Rugh 1948, Kaplan 1979). No ova remained in the oviducts of three females that oviposited in the lab, and only immature follicles were detected on their ovaries. This indicates that all mature ova are oviposited by females, so yolked ovarian compliments may accurately estimate annual fecundity in this species.

There was a moderate positive correlation ($r^2 = 0.41$, P = 0.01) between female age and clutch size (Fig. 5), and a strong and highly significant positive correlation ($r^2 = 0.77$, P < 0.0001) between female SVL and clutch size (Fig. 5B). There was a moderate negative relationship ($r^2 = -0.46$, P = 0.008) between clutch size and mean ovum diameter (Fig. 6).

DISCUSSION

This study is the first to document age distribution in a population of *Rana areolata*. Correlations between age distribution, age at sexual maturity, SVL distribution, and fecundity can reveal important data on factors affecting population characteristics in *R. areolata*. Several other studies have reported on, and indicate considerable var-

iation of SVL in populations of *R. areolata*. In another study in Williamson County, Illinois (ca. 10 km from my study site), Smith et al. (1948) reported no mean SVLs, though they reported modal SVLs of 100 mm (males) and 95 mm (females). They reported maximum SVLs for both males (117 mm) and females (118 mm) that exceeded my size maxima (90 mm and 102 mm, respectively). Smith et al. (1948) noted the presence of very small, yet sexually mature males (minimum SVL = 64 mm) and females (minimum SVL = 75 mm) in their sample. Small, sexually dimorphic males (minimum SVL = 71 mm) and females (minimum SVL = 80 mm) were present in my sample, though none of these was found in amplexus. The size maxima (90 mm for males, 102 mm for females) reported here are smaller than the maximum size (114 mm) reported by Conant and Collins (1991), though both male and female size maxima reported by Smith, et al. (1948) are larger. Bragg (1953) reported mean SVLs of 81.8 mm (range = 61–95 mm, n = 16 males, one female), 92.3 mm (range = 72–108 mm, n = 15 males), and 80.6 mm (range = 67–89 mm, n = 9 males, one female) from three samples collected in Oklahoma and Louisiana. Elsewhere, reported *R. areolata* size maxima are 99 mm in Missouri (Powell et al. 1982), 104 mm for males, 108 mm for females in Indiana (Minton 1972), and 110 mm in Kansas (Collins 1993).

Other studies of correlations in anuran age and size have suggested that larger amphibian species tend to live longer than smaller ones (Duellman and Trueb 1986). While *R. areolata* is one of the largest North American *Rana* species, the maximum skeletochronologically estimated age of 5 yr (this study) is not much greater than those reported for small and medium sized species. Two medium-sized species, *R. pipiens* and *R. sphenocephala*, reach 4 yr in Quebec (LeClair and Castanet 1987) and southern Illinois (Redmer 1999), respectively. However, a small species, *R. sylvatica*, reaches 5 yr in Quebec (Bastien and LeClair 1992), 3–4 yr in Maryland and Virginia (Berven 1982a, 1990), and 5 yr in southern Illinois (Redmer 1999). Conversely, Shroeder and Baskett (1968) reported that wild *R. catesbeiana* (the largest North American species) could reach ages greater than 6 yr, and Platz et al. (1997) reported that *R. subaquavocalis* (a large species) reached a maximum age of 10 yr. My sample was relatively small, but minimum age of sexual maturity was 2 yr for males and 3 yr for females. If all sexually mature age classes present in the population were represented in this sample, males have a maximum of four years of reproductive life, while females have a maximum of three years of reproductive life. It should be emphasized that lon-

gevity alone may not be indicative of reproductive potential. In this study, age was less correlated with fecundity than was SVL, suggesting that annual reproductive potential and fitness are more effected by growth than by age. Smith et al. (1948) reported a range (3192–6807) of clutch sizes (n = 6) that nearly matches the range (3208–6807) in my study (n = 15), but they gave no mean clutch size. Other studies of fecundity in this species reported some variation in clutch sizes. Smith (1934) estimated 7000 eggs for Kansas populations. Bragg (1953) reported one clutch of 3801, and estimated (based on water displacement) a range of 2000–4500 eggs for other clutches from an Oklahoma population. Trauth et al. (1990) reported a clutch of 2233 eggs from an Arkansas female, the clutch and SVL (66.8 mm) of that specimen were much smaller than any female or clutch reported in this study.

Several previous studies reported ovum sizes of *R. areolata*. Smith, et al. (1948) reported embryo (the eggs in their sample were oviposited) diameters of 1.91–2.18 mm from Williamson County, Illinois *R. areolata*, a range similar to the sample reported herein (range = 1.80–2.20, mean = 2.05 mm). Bragg (1953) reported mean embryo (some of which had developed to gastrula stage) diameters of 2.0 mm (range = 1.7–2.4 mm), 2.1mm (range = 1.0–2.2 mm), and 2.2 mm (range = 1.8–3.8 mm) for three Oklahoma samples. Volpe (1957) reported a mean embryo diameter of 1.84 mm (range = 1.67–2.18 mm) for the related *R. capito* from Mississippi. All of these ovum and embryo sizes are similar to those reported here. However, this is the first study to confirm a negative correlation between ovum size and clutch size.

In amphibians, several factors are known to contribute to larval fitness and recruitment of metamorphs. Among these factors are ovum size, competition, growth rate, and mass at metamorphosis (Berven and Gill 1983, Berven 1990, Parris and Semlitsch 1998, Semlitsch et al. 1988, Smith 1987). Also, age structure in adult populations of amphibians may be strongly influenced by variation in larval survival and recruitment (Berven 1990, Semlitsch et al. 1996). Life history and reproductive parameters of Ranid frogs may be subject to geographic variation (Berven 1982a, 1982b, 1988, Berven and Gill 1983). Future studies should investigate further how performance in these larval and juvenile life-history stages affect adult populations of *R. areolata*. Although my sample was relatively small, and collected in only one year, my data indicate that female *R. areolata* are slow to reach sexual maturity, and once they do so have only 2–3 yr of potential reproductive life. Stochastic events (such as drought) that cause tadpole mortality could indirectly limit reproductive potential, and in turn could contribute to localized fluctuations in the adult population, or localized declines.

Skeletochronology is an effective method for estimating age in populations of *Rana areolata* and other amphibian species, but when used in single years tells little about population trends. It would be better if this technique were used over several years to detect fluctuations in age structure between years (Friedl and Klump 1997). Additional studies should continue to combine methods (such as skeletochronology) for determining demography and age of adult populations with studies of reproductive traits, and should also be expanded to examine relationships between larval and adult life stages. Such comprehensive studies may help amphibian biologists to better track population trends and to identify reasons why *R. areolata* and other species may be in regional decline.

ACKNOWLEDGEMENTS

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