

**David A. Pike, Ligia Pizzatto, Brian A. Pike, and Richard Shine. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. *Ecology* 89:607-611.**

Appendix A: Details of the model used to estimate annual rates of juvenile survival in lizards, snakes, and turtles.

We use a two-phase exponential distribution to model the mortality of individuals, in which we assume that the instantaneous mortality rates of juveniles and of adults are constant over time. Let  $a$  denote the age at which an individual becomes an adult (i.e., can reproduce). Throughout this appendix, we will use the term 'age' to mean the time, in years, since an individual was born (in the case of ovoviviparous organisms), or since an individual's egg was laid (in the case of oviparous organisms). We want each phase of life to have the property that the probability of an individual surviving from age  $x$  to age  $x + 1$  is constant, as long as the age  $x$  and age  $x + 1$  individuals fall in the same life phase. Because this is very similar to the memoryless property exhibited by the exponential distribution, we model each phase with an exponential distribution.

Let  $\lambda_j$  and  $\lambda_A$  denote the parameters of the exponential distribution for the juvenile and adult phases, respectively. Then our probability density function for the mortality is given by

$$f(x) = \begin{cases} 0 & x < 0 \\ \lambda_j e^{-\lambda_j x} & 0 \leq x \leq a, \\ k\lambda_A e^{-\lambda_A x} & a < x \end{cases}$$

where  $k = e^{(\lambda_A - \lambda_j)a}$  ensures that  $\int_{-\infty}^{\infty} f(x) dx = 1$ . The probability of an individual dying in less than or equal to  $t$  years is given by our cumulative distribution function,

$$F(t) = \int_{-\infty}^t f(x) dx = \begin{cases} 0 & t \leq 0 \\ 1 - e^{-\lambda_j t} & 0 < t < a. \\ 1 - ke^{-\lambda_A t} & a < t \end{cases}$$

Then the probability of an individual surviving greater than  $t$  years is given by the expression

$$1 - F(t) = \begin{cases} 1 & t \leq 0 \\ e^{-\lambda_j t} & 0 < t < a. \\ ke^{-\lambda_A t} & a < t \end{cases}$$

As a result, the probability of an individual surviving at least  $x+1$  years, given that they have survived  $x$  years, can be calculated to be  $s_j = e^{-\lambda_j}$  when at both times the individual is a juvenile, and  $s_A = e^{-\lambda_A}$  when at both times the individual is an adult. This is exactly the memoryless property we desire.

We wish to relate the number of offspring born every breeding cycle to the number of adult females in the population in order to be able to express some relationship between the juvenile and adult survival rates. There are multiple ways to do this, so we choose one.

We consider a simple model, in which all adult females will produce a set number of offspring each year that they are alive. This is appropriate for species that have a concentrated clutch-laying period every year, but may be less appropriate for species that lay clutches year-round. Consider the set  $S$  of all individuals born in the same year. Let  $P_i$  be the number of individuals from  $S$  still living after  $i$  years, where  $i \geq 0$ . Then we will expect, if  $P_0$  is large enough, to have:

$$P_i = P_0(1 - F(i)) = \begin{cases} P_0 s_J^i & i < a \\ P_0 s_J^a s_A^{i-a} & i \geq a \end{cases}.$$

We assume our population to be stable not only in the sense that the total number of living individuals is constant across years, but also in the sense that the number of age  $i$  individuals in the population is constant across years, for all  $i \geq 0$ . This assumption gives us  $P_i$  as the number of age  $i$  individuals in any given year.

We can now calculate the number of offspring produced per year. Let  $c$  denote the number of offspring produced per clutch, and let  $n$  denote the number of clutches per year per female. For oviparous organisms, note that we may take  $c$  to be the number of eggs produced per female per year if we consider individuals in eggs to be living, and allow  $s_J$  to account for eggs that are laid but do not hatch. Let  $f$  be the percentage of female individuals in the adult population. We assume that each adult female in the population produces  $cn$  offspring per year as long as the individual lives (i.e., senescence never reached). There will be  $f \sum_{i=0}^{\infty} P_{a+i}$  adult females in the population and

$cnf \sum_{i=0}^{\infty} P_{a+i}$  individuals born per year. But  $P_0$  is the number of age 0

individuals in any given year, so:

$$\begin{aligned} P_0 &= cnf \sum_{i=0}^{\infty} P_{a+i} \\ P_0 &= cnf P_0 s_J^a \sum_{i=0}^{\infty} s_A^i \\ P_0 &= cnf P_0 s_J^a (1 - s_A)^{-1} \end{aligned}$$

since  $\sum_{i=0}^{\infty} s_A^i$  is a geometric series with  $s_A < 1$ . Now, dividing through by  $P_0$

and solving for  $s_J^a$  gives the equation:

$$s_J^a = \frac{1 - s_A}{cnf}.$$

This equation relates the survival rate of juveniles to adulthood to the yearly survival rate of adults, the number of offspring produced per clutch, the number of clutches per female per year, and the proportion of females in the adult population. Solving for  $s_J$  gives an estimate for the annual survival rate of juveniles

$$s_J = \left( \frac{1 - s_A}{cnf} \right)^{1/a},$$

under the assumptions of our model. Note that for the purposes of this paper, we have assumed  $f = \frac{1}{2}$ , so our estimate is

$$s_J = \left( \frac{2(1 - s_A)}{cn} \right)^{1/a}.$$

It is clearly unrealistic to assume that juveniles have a constant rate of survival throughout their juvenility. Instead, we have attempted to only

estimate a rate at which juveniles die before they reach adulthood, and then use our estimate to find an average, of sorts, of the annual survival rate of juveniles; this is how  $s_J$  should be interpreted.