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Population estimators and adult sex ratio for a population of *Bolitoglossa altamazonica* (Caudata: Plethodontidae)

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Bolitoglossa altamazonica is the species of plethodontid salamander with the widest distribution in the tropics. However, while aspects related to population size, survival rates, recruitment, sex ratios along with other life history traits are well documented for temperate salamanders, such information is relatively scarce for tropical species. We conducted an intensive capture-recapture study on a population of *B. altamazonica*. We used the Jolly-Seber method to estimate three parameters (size, recruitment and survivorship) for the population as a whole, as well as for males, females and juveniles separately. All these parameters varied monthly for each class and the entire population. Juvenile recruitment occurred between november and july. Survivorship of juveniles increased when there was no recruitment at all. The adult sex ratio during the breeding season was significantly biased towards females (up to 1:3 depending on the month).

Key words: population size; recruitment; salamanders; sex ratio; survivorship.

Estimadores de población y razón de sexos en una población de *Bolitoglossa altamazonica* (Caudata: Plethodontidae). *Bolitoglossa altamazonica* es la especie de pletodóntido con distribución más amplia en los trópicos. Sin embargo, mientras que los aspectos relacionados con el tamaño de la población, tasa de supervivencia, reclutamiento, razón de sexos y otras características de la historia vital están bien documentados en salamandras de zonas templadas, la información para especies tropicales es relativamente escasa. Llevamos a cabo un estudio intensivo de marcaje-recaptura en una población de *B. altamazonica*. Utilizamos el método de Jolly-Seber para estimar tres parámetros (tamaño, reclutamiento y supervivencia) tanto para el conjunto de la población como para machos, hembras y juveniles por separado. Todos los parámetros estimados experimentaron variaciones mensuales en cada una de las clases así como en el conjunto de la población. El reclutamiento de los juveniles sucedió entre noviembre y julio. La supervivencia de los juveniles se incrementó cuando no existía reclutamiento. La razón de sexos de la población adulta durante el periodo reproductor estuvo significativamente sesgada en favor de las hembras (hasta 1:3 dependiendo del mes).

Key words: razón de sexos; reclutamiento; salamandras; supervivencia; tamaño de población.

Reports on declining and disappearing amphibian populations have received a great deal of attention in recent years (PECHMANN & WILBUR, 1994). These population fluctuations are believed to be the result of natural events (PECHMANN & WILBUR, 1994) or environmental perturbations (POUNDS *et al.*, 1997), and differentiating problematic declines from natural fluctuations in populations is an issue of particular difficulty in applied ecology (PECHMANN *et al.*, 1991). One-third of all amphibian species worldwide is endangered or threatened with extinction (STUART *et al.*, 2004). Efforts to understand the causes of this alarming decline, known as the global amphibian crisis, have focused primarily on frogs; comparatively little attention has been paid to salamanders (LIPS, 1998; PARRA-OLEA *et al.*, 1999; WHITFIELD *et al.*, 2007). A reason for this bias includes the fact that most salamanders are secretive in nature, so populations trends may not be as apparent as in frogs, but the global amphibian crisis, usually discussed in terms of frogs, clearly involves neotropical salamanders as well (ROVITO *et al.*, 2009).

Declining trends are impossible to detect without long-term abundance-based data on population densities collected by using a consistent methodology. Although those data sets are exceptionally rare, they are critical to understand the full extent of the global amphibian crisis (WHITFIELD *et al.*, 2007). An assessment of the status and conservation of amphibians requires an expanded, regional perspective (HECNAR & M'CLOSKEY, 1996); however, few estimates of amphibian natural history parameters exist against which to judge the extent of additional mortality (BLACKWELL *et al.*, 2004).

Population size indicates how the reproductive health for a given population is, and survivorship often explains a large portion of an individual's lifetime reproductive success (OLGUN *et al.*, 2001). Therefore, analyses of the variation of life history parameters such as survival rates and recruitment over time are of major importance not only for understanding the life history of a species (FLATT *et al.*, 1997), but also for providing an expanded regional perspective for conservation and management (BLACKWELL *et al.*, 2004).

In ecological studies, the adult sex ratio, defined as the proportion of reproductive females and males within the breeding population, is considered a key parameter in understanding sexual selection, mating behaviour, and population dynamics (KVARNEMO & AHNESJÖ, 2002). According to classical sex allocation theories, in natural populations a balanced sex ratio should be maintained in the long term by a selective advantage to the parents producing the rarest sex (RANTA *et al.*, 2000). However, in amphibians, the relative numbers of sexually active males and females show large interspecific variations depending on the mode of reproduction, mating system and resource distribution (ZUG *et al.*, 2001).

All neotropical salamanders belong to the tribe Bolitoglossini (family Plethodontidae); these salamanders have direct development of young inside terrestrially laid eggs (WAKE, 1966). The supergenus *Bolitoglossa* contains about two-thirds of plethodontid species and about 40% of all species of salamanders (AMPHIBIAWEB, 2011). *Bolitoglossa altamazonica* occurs on the eastern slopes of the Andes from Venezuela and Colombia, through Ecuador, Peru and Bolivia, and as far east as eastern Brazil. Because of its wide distribution and presumed large populations, *B. altamazonica* is listed as Least Concern in the IUCN Red List (AZEVEDO-RAMOS *et al.*, 2009).

The main goals of this study were to examine three population parameters (size, survivorship and recruitment) for a population of *B. altamazonica* and to evaluate whether the adult sex ratio is balanced and constant through time. The present study contributes to the knowledge of amphibian life history by documenting temporal population parameters of a population of *B. altamazonica*. This dataset provides the best opportunity to examine changes in salamander populations over time, thus serving as a reference for comparison to populations in other localities from Colombia and along its distribution range.

MATERIALS AND METHODS

The study site, Jardín Botánico de Villavicencio, is a local natural reserve since 1983 located in Villavicencio City, Meta, Colombia (04º 09' 09'' N, 73º 39' 15'' W) at 640 m above sea level. It is a humid tropical forest (HOLDRIDGE *et al.*, 1971) with mean annual rainfall, temperature and relative humidity of 4531 mm, 25.9ºC and 76%, respectively. The rainfall regime is unimodal with a maximum peak of rains from May to June. The dry season usually extends from December to March (data recorded from the nearest weather station: Vanguardia – Instituto de Hidrología, Meteorología y Estudios Ambientales de Colombia).

At the study site, we established a 7300 m^2-plot. We captured salamanders within this plot by visual encounter (CRUMP & SCOTT, 1994; ANGULO *et al.*, 2006). Two experienced researchers looked for salamanders during eight nights (19:00-02:00), monthly from April 2008 to November 2008 with an additional sampling performed in January 2009. All surveys were conducted at night because the focal species is nocturnal and surface activity occurs at night. We marked animals using freeze branding with liquid nitrogen (DAUGHERTY, 1976). Individual identification was achieved by combinations of marks in fifteen body locations (modified from NISHIKAWA & SERVICE, 1988), five on each side of the body and five mid-dorsally according to the following distribution: anterior and posterior to the fore limb, midbody, anterior and posterior to the hind limb. We measured snout-vent length (SVL: tip of the snout to posterior margin of the vent) using a vernier calliper after restraining the salamanders in a plastic bag. Adults were sexed in accordance with their size (SVL) and secondary characters; during the breeding period, mature males had an enlarged, disc-like mental gland in the anterior region of the lower jaw (SVL: 34.58-44.86 mm) whereas mature females were gravid (SVL: 36.34-57.84 mm). We used these SVLs as a reference for sexing individuals out of the breeding season; however, because of the big overlap in size between sexes, only large females (SVL > 44.86 mm) and small males (SVL < 36.34 mm) could be sexed in the field. All specimens with an SVL below 34.00 mm without sexual secondary characters were classified as juveniles. We returned all animals to the spot where we captured them after data collection and marking.

The primary goal of the mark-recapture analysis was to estimate population size, survival and recruitment. In an open population that is affected by mortality and migration, variable survival rates are more biologically realistic than fixed ones (DONNELLY & GUYER, 1994; KREBS, 1999). Survival can be estimated using standard mark-recapture methodology (LEBRETON *et al.*, 1992). Local survivorship represents the probability of surviving from month (i) to month (i + 1), and is affected by both mortality and permanent emigration. Local recruitment is the number of new animals in the population at time i per animal in the population at time i - 1 (PRADEL, 1996), and it includes in situ reproduction and immigration. We included sex and age as grouping factors in the model selection procedure to allow for testing sex- and age-specific effects on the parameters of interest. We analyzed mark-recapture data using Cormack Jolly-Seber (CJS) and Pradel survival and recruitment extensions of Program MARK version 5.0 (WHITE & BURNHAM, 1999). We used an overall model selection procedure before parameter estimation. Ten a priori candidate models offered different biological representations of the role of capture probability among sexes and ages (adult or juvenile). Rather than including all possible permutations in the primary model selection procedure, we initially tested four models to evaluate sex differences in detectability and survival; then, we tested four additional models accounting for possible age differences in these variables. Parameters in the candidate models were either allowed to vary over time or to remain constant. Model selection was based on the small-sample Akaike's information criterion (AICc; BURNHAM & ANDERSON, 2002). Some parameters were estimated after 15 000 simulations using Markov chain Monte Carlo (MCMC), keeping all the other parameters that did not have standard errors extremely high or low fixed. We used the Jolly-Seber original model (JOLLY, 1965; SEBER, 1965) to estimate population size, since program Mark never reached numerical convergence. Adult sex ratio was expressed as the relative proportions of estimated mature males and females, and deviations from a 1:1 ratio were tested through a Chi-square test.

RESULTS

We captured 880 individuals of *B. altamazonica*, 244 of which were recaptured for a total of 1124 captures in nine months. Monthly captures regardless of sex or age ranged from 64 to 184 individuals, and fluctuated following the same pattern as rainfall, with a peak of captured salamanders in June (Fig. 1). Because of the intense sampling, frequency of captures of new individuals declined rapidly over time, in spite of which we captured new individuals in all months.

Table 1: Model rankings to evaluate sex and age effects on survival (Phi) and detectability (p), using the Cormack-Jolly-Seber (CJS) extension, and age and time effects on survival and recruitment (f), using the Pradel extension, in a population of *Bolitoglossa altamazonica*. Models are listed in decreasing order of support using Akaike's Information Criterion. g = gender/age-dependent, t = time-dependent.

Extension	Model	AICc	Delta AICc	AICc weight	Model likelihood	Deviance
CJS (Sex)	Phi(t) p(t)	203.87	0.00	0.669	1.00	20.85
	Phi(g*t) p(g*t)	206.41	2.53	0.188	0.28	12.81
	Phi(g*t) p(t)	207.84	3.97	0.092	0.137	18.52
	Phi(t) p(g*t)	209.09	5.21	0.049	0.074	19.76
CJS (Age)	Phi(t) p(g*t)	1763.93	0.00	0.882	1.00	239.94
	Phi(g*t) p(g*t)	1768.23	4.299	0.103	0.116	229.49
	Phi(t) p(t)	1772.19	8.263	0.014	0.016	264.82
	Phi(g*t) p(t)	1777.36	13.426	0.001	0.001	253.37
Pradel	Phi (t) p(g*t) f(g*t)	5444.219	0.00	0.984	1.00	242.66
	Phi (t) p(g*t) f(t)	5452.48	8.26	0.016	0.016	257.28

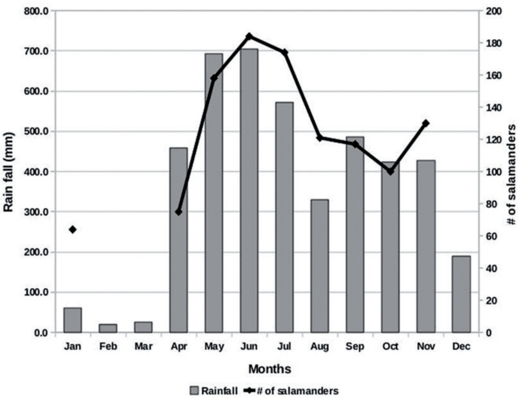

Figure 1: Monthly variation in the number of captured salamanders (black line) and its relationship with rainfall values (grey bars).

From the set of models used to evaluate sex effects on survival and detectability, the model that fitted better into our capture-recapture history was that considering both parameters to vary over time without effects of sex (Table 1). Thus, we did not include in subsequent analyses the effects of sex on these two variables. The second set of models, used to evaluate age effects on survival and detectability, supported the time-varying detectability, revealing differences between ages in detectability but not in survival (Table 1). Finally, the comparison of the two models to evaluate age and time effects on recruitment showed that this parameter varied as a function of both factors (Table 1).

Population size estimates fluctuated between months, ranging from 582 in May to a maximum of 2165 individuals in October. Survivorship also fluctuated between months, with the highest trustable estimate in July. Although the estimated survivorship for September was higher than that of July, we disregarded it because of its large standard error; such a high value for survivorship is a mathematical artefact produced by the large number of individuals marked in October in contrast with the low number of individual marked during September (Table 2).

Using the maximum number of salamanders estimated by the Jolly-Seber method, the population density within the studied plot would be 0.23 salamanders / m^2. For density estimation, we used the population size obtained in October (highest value) because a good number of specimens were already marked by that month (752), and salamanders were highly active because of favourable weather conditions, allowing us to calculate population density without underestimations.

For estimating juvenile population parameters, we used 412 marked specimens and 69 recaptures, for a total of 480 captures. We identified an individual as juvenile in May (SVL = 34.6 mm), but when we recaptured it 30 days later it showed a visible and completely developed mental gland (SVL = 38.24 mm). Between-months recruitment was highly variable (Table 3). The highest juvenile recruitment occurred in June and July, while

Table 2: Population size (N) and survival (Phi) estimates (± SE) for a population of *Bolitoglossa altamazonica*. No data from January were calculated because, due to the absence of sampling in December, they did not meet the Jolly-Seber method requirement of consecutive samplings.

Month	N	Phi
April	-	0.342 (± 0.107)
May	582 (± 253)	0.847 (± 0.140)
June	1348 (± 350)	0.779 (± 0.125)
July	1344 (± 280)	0.880 (± 0.162)
August	1267 (± 275)	0.830 (± 0.171)
September	776 (± 150)	1.950 (± 0.196)
October	2165 (± 896)	0.825 (± 0.362)
November	1298 (± 560)	0.281 (± 17.995)
January	-	-

Table 3: Juvenile and adult recruitment (f) and detectability (p) (± SE) in a population of *Bolitoglossa altamazonica*.

Month	Adults		Juveniles	
	f	p	f	p
May	1.145 (± 0.276)	0.174 (± 0.102)	7.558 (± 1.709)	0.242 (± 0.000)
June	0.825 (± 0.219)	0.152 (± 0.050)	0.061 (± 0.124)	0.238 (± 0.174)
July	0.122 (± 0.274)	0.136 (± 0.037)	0.320 (± 0.127)	0.105 (± 0.037)
August	-0.008 (± 0.004)	0.127 (± 0.033)	0.011 (± 0.223)	0.111 (± 0.0321)
September	0.268 (± 0.123)	0.200 (± 0.045)	0.006 (± 0.062)	0.077 (± 0.017)
October	0.407 (± 0.182)	0.120 (± 0.027)	0.006 (± 0.089)	0.071 (± 0.016)
November	0.327 (± 0.227)	0.082 (± 0.039)	0.024 (± 0.093)	0.064 (± 0.015)
January	0.027 (± 1.085)	0.104 (± 0.021)	0.011 (± 0.130)	0.124 (± 0.055)

no new juveniles entered the population between September and October. We did not take into account juvenile recruitment estimates in May because of the high standard error. We performed estimates for adults from 468 individuals, 175 of which were recaptured for a total of 643 captures. Adult recruitment was highest in June and dropped along with the rainfall; in August-September no new adults entered the population (Table 3).

Using the 100 males and 245 females captured during the breeding season, which runs from January to July (GUTIÉRREZ-LAMUS, 2009), we found a significantly female-biased sex ratio that ranged between months from 1:2 to 1:3 (Table 4).

DISCUSSION

The results from this study are the first of its kind for *B. altamazonica* and contribute to the knowledge about this population in regards to its size, survivorship, recruitment and adult sex ratio.

The key estimates for many ecologists using the CJS model on capture-recapture data are the survival rates, with the capture probabilities often viewed as little important nuisance parameters (PLEDGER *et al.*, 2003). Numerous authors have suggested that this assumption is met as capture probability is likely to vary among demographic groups over time (WILLSON *et al.*, 2011). The mistake of assuming constant capture probability when variation actually exists can bias estimates of abundance or recruitment (POLLOCK *et al.*, 1990; BAILEY *et al.*, 2004). Imperfect detectability also extends to the estimation of survival (MAZEROLLE *et al.*, 2007). Adjusted population estimates, which estimate the "true" population based on capture-recapture techniques, are labour-intensive but may yield a more accurate picture of the number of salamanders present in a population (JUNG *et al.*, 2000).

Table 4: Chi-square test to analyse the sex ratio obtained in a population of *Bolitoglossa altamazonica*. The null hypothesis is a one-to-one sex ratio. *P*-values in bold face are significant.

Month	N (males)	N (females)	Sex ratio	χ^2 (d.f. = 1)	*P*
April	17	31	1:1.8	4.0833	**0.0433**
May	17	46	1:2.7	13.3492	**0.0000**
June	29	67	1:2.3	15.0417	**0.0003**
July	23	64	1:2.8	19.3218	**0.0000**
January	14	37	1:2.6	10.3726	**0.0013**
Total	100	245	1:2.45	60.9420	**0.0000**

According to recruitment estimates, most juveniles enter the population in July, and recruitment gradually decreases during subsequent months along with rainfall. Juvenile recruitment was almost null between August and October, but in November new young individuals entered the population again. Nevertheless, such results can be sample size artefacts because we marked young individuals during those months when recruitment estimated by Pradel method was close to zero. The method does not provide estimates for the first month of sampling. For this reason, we believe that juvenile recruitment occurs continually from November through July. The intensity of recruitment depends on the effective size of the breeding population and the survivorship of the eggs (DUELLMAN & TRUEB, 1994), as well as the volume of captures. According to the estimates for both adults and juveniles, most recruitment occurs between June and July, when rainfall reaches maximum levels. On the other hand, new adults do not enter the population when rainfall decreases (August-September).

Several reasons could have caused the fluctuations in our estimates; first, our inability to find and mark brooding females; second, sampling during rainy nights when activity notably decreased; third, the behavioural thermoregulation demonstrated in plethodontids (SPOTILA, 1972; FEDER, 1982), consisting in that animals select optimal temperatures by moving to preferred parts of the gradient. If optimal temperatures were achieved in the litter, we could hardly find animals there. Fourth, the cutaneous gas exchange may account for more than 90% of the exchange in plethodontids, which might force animals to use microhabitats with adequate humidity and temperature in order to minimize the risk of water loss (SPOTILA 1972). Salamander capture probabilities are influenced by a number of factors, including site-specific characteristics, weather conditions and hour of day (JUNG *et al.*, 2000). Nevertheless, long-time monitoring studies in species such as *Ambystoma maculatum* (BLACKWELL *et al.*, 2004) and *Ambystoma tigrinum* (WHITEMAN & WISSINGER, 2005) have revealed fluctuations in population size between years.

After comparing rainfall data and animal abundance, we detect an obvious relationship between population density and weather conditions. We obtained the greatest values for captures, population size and recruitment when rainfall levels were high. It has been generally accepted that moisture, as expressed in the amount and distribution of rainfall, exerts the greatest influence on the distribution of organisms in tropical environments (AUBERT DE LA RÜE *et al.*, 1957; RICHARDS, 1957 in VIAL, 1968). Similar responses to annual distribution of rainfall have been reported for *Bolitoglossa subpalmata* (VIAL, 1968), *Batrachoseps* spp. (HENDRICKSON, 1954; ANDERSON, 1960) *Aneides lugubris* (ROSENTHAL, 1957) and *Ensatina* spp. (STEBBINS, 1954).

Available information on population densities of salamander comes from a limited number of studies that employ a variety of techniques (VIAL, 1968). Among neotropical salamanders, densities have been reported only for *B. subpalmata*, ranging from 0.0756 to 0.9097 individuals / m^2 (VIAL, 1968), being the present study the second report so far. In general, there is a great variation in local population densities for plehodontids; TEST & BINGHAM (1948) reported 0.0496 individuals / m^2 of *Plethodon cinereus*, and then BURTON & LIKENS (1975) estimated for the same species densities ranging from 2.3670 to 2.5830 individuals / m^2. Estimated densities for other salamanders include 0.0070 individuals / m^2 in *Plethodon yonahlossee*, 0.0220 individuals / m^2 in *Plethodon jordani* (GORDON *et al.*, 1962), 0.4180-0.8440 individuals / m^2 in *Plethodon glutinosus* (SEMLITSCH, 1980), 0.4051-0.4989 individuals / m^2 in *A. lugubris* (ANDERSON, 1960), 0.10-0.25 individuals / m^2 in *Aneides aeneus* (GORDON, 1952) and 0.1482-0.1729 individuals / m^2 in *Ensatina eschscholtzii* (STEBBINS, 1954). Unfortunately, most reports on population densities of plethodontids were calculated before herpetologists could deal with imperfect detection through more sophisticated approaches, which ultimately served to avoid repercussions of poor detection on the assessment of population size, population density and any other vital rate.

Survivorship is dependent upon finding an adequate refuge to obtain protection from predators and desiccation (SMYERS *et al.*, 2002). HUSTING (1965) reported survival rates of 0.72 for males and 0.60 for females in a Michigan population of *A. maculatum*, and BLACKWELL *et al.* (2004) also reported high survival rates in a population of this species from Alabama, which led them to the conclusion that adult survival was the largest contributor to population growth in *A. maculatum*. In the most comprehensive study of survivorship of plethodontids, ORGAN (1961) calculated life tables for five species of *Desmognathus* and showed that there was a progressive increase in early survival rate from the most aquatic species, *D. quadramaculatus*, to the most terrestrial one, *D. wrighti*.

Survivorship estimates for *B. altamazonica* including all captured animals are quite high and did not vary too much. However, we must take into account that we calculated apparent survivorship and not real survival rates, because without conducting a more exhaustive study it was not possible to attribute losses in the population to deaths or emigration accurately. Generally, adult survival is likely to be more important than recruitment for population persistence, because it determines how long a population can persist without recruiting new individuals (SCHMIDT *et al.*, 2005).

The sex ratios obtained during the present study showed a predominant proportion of females in the breeding population, which is in agreement with data reported for several species of plethodontid salamanders like *Plethodon vehiculum*, *Plethodon dunni* (DUMAS, 1956), *P. yonahlossee* (POPE, 1950), *D. quadramaculatus* (ORGAN, 1961) and *A. maculatum* (BLACKWELL *et al.*, 2004). This unbalanced sex ratio cannot be attributed to differential mortality, as we found homogeneity across sexes and ages in survival rates. A possible reason to explain our result would be that *B. altamazonica* males do not exhibit philopatry. On the contrary, other plethodontids such as *P. cinereus* (TEST & BINGHAM, 1948), *A. aeneus* (GORDON, 1952), *Desmognathus fuscus*, *Desmognathus carolinensis*, *D. wrighti* (ORGAN, 1961) and *Eurycea wilderae* (BRUCE, 1988) show sex ratios unbalanced in favour of males. Finally, for *B. subpalmata* (VIAL, 1968) and *Bolitoglossa nicefori* (ORTEGA *et al.*, 2009) there is no bias between sexes, even though they belong to the same genus as our study species. Differences in sex ratios for species belonging to the same genus have been also reported in *Plethodon* and *Desmognathus*.

Although sex ratio varied slightly among months, there was on average three females per male. In some species of *Desmognathus*, variations in sex ratio over time are due to the fact that females move to the aquatic habitat during brooding. That is not the case for *B. altamazonica*, whose nesting microhabitats offer optimal conditions and are commonly used also by non-reproducing members of the population. Such a pattern of habitat use has been described also for *B. subpalmata* (VIAL, 1968).

Data reported here are a baseline essential for evaluating population changes over time, and for assessing relationships between salamander populations and environmental factors. The present study can be used as a starting point for comparison to other *B. altamazonica* populations along the wide range of distribution of the species; such comparisons will be useful when planning mitigation or restoration projects.

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