

# Temporal variation in adult sex ratio in a population of the terrestrial salamander *Speleomantes strinatii*

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The adult sex ratio of a population of *Speleomantes strinatii* living in an underground habitat was studied for 12 consecutive years by temporal removal sampling. Capture probabilities of males (0.72) and females (0.69) were similar and yielded highly reliable sex ratio values. The adult sex ratio, expressed as the proportion of males, was significantly male-biased (mean 0.57, bootstrap 95% confidence intervals 0.53–0.65) and remained relatively constant during the study. A negative relationship was observed between adult sex ratio in one year and the abundance of juveniles in the following one ( $P=0.02$ ), suggesting that an excess of males limited juvenile recruitment and therefore influenced population dynamics.

**Key words:** capture probabilities, cave habitat, Plethodontidae, population dynamics, recruitment

In ecological studies the adult sex ratio (ASR, 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 (Yablokov, 1986; Kvarnemo & Ahnesjö, 2002). According to the classical theories of sex allocation, 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 (Fisher, 1930; 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, the mating system and the overall distribution of resources (Zug et al., 2001). Moreover, large intraspecific variations were observed both seasonally and geographically (e.g. Arntzen, 2002). In the salamander family Plethodontidae, which is found in the Americas, southern Europe and Korea, the sex ratio of immature age classes seems balanced (but see Leclair et al., 2006), while a male-biased departure from a 1:1 proportion is sometimes observed in adults, for instance in *Desmognathus* (Organ, 1961) and *Eurycea* (Bruce, 1988). A higher death rate in breeding females, probably occurring during the relatively long period of clutch guarding typical of these salamanders, was suggested as the main cause of the observed sex ratio pattern (Organ, 1961). However, clear evidence of sex-related differential mortal-

ity is lacking in plethodontid salamanders (Bruce et al., 2002; Leclair et al., 2006). In addition, there may be difficulties in the estimation of ASR from single or few field samples, because males and females may show different behaviour or activity rates and consequently may have different probabilities of being detected and captured (Schmidt, 2004; Donald, 2007).

In this study, a population of the terrestrial plethodontid salamander *Speleomantes strinatii* (Aellen, 1958) was studied for 12 consecutive years in north-west Italy, and the abundance of adult individuals was estimated each year on the basis of sex-specific capture probabilities (CP). Abundance estimates were highly reliable, allowing strong inferences that are difficult to obtain when uncorrected counts or indexes are used (Anderson, 2001; Schmidt, 2004). This study addressed two different questions concerning ASR in the *S. strinatii* population: 1) is the population ASR balanced and constant through time, and 2) is there an apparent relationship between the ASR and population dynamics?

*Speleomantes strinatii* is a medium-sized (total length <115 mm) plethodontid salamander endemic to southern France and north-west Italy. It is found on humid rock outcrops, in forest leaf litter and in caves (Lanza et al., 2005). The aquatic larval stage is lacking and, during winter, females lay about ten large eggs that are attended until hatching (Lanza et al., 2005). Recruitment is seasonal and three immature groups (newborns, yearlings and subadults) may be recognized as separate age classes (Salvidio & Pastorino, 2002). Males become sexually active at a snout–vent length (SVL) of 50 mm when a mental gland becomes conspicuous. A previous study based on dissections (Salvidio, 1993), demonstrated that females become sexually mature at an  $SVL \geq 58$  mm, and probably at an older age than males. Females, however, outgrow males in maximum size by about 7% (Salvidio & Bruce, 2006).

The study site is an artificial cavity excavated during World War II near Busalla (Genova, NW Italy) and naturally colonized by the salamanders (Salvidio et al., 1994). During the summer, salamander activity is inhibited by hot and dry weather and animals concentrate in underground habitats, where they are easily captured (Salvidio, 2001). Population abundances were estimated from 1996 to 2007 with a standardized temporary removal experiment (White et al., 1982), with three removal samples obtained every other day in July. The population was considered closed as the sampling interval was short (i.e. within 96 hours) and dispersion from the cave was prevented by weather conditions. Salamanders were sexed, measured and kept in ventilated plastic boxes inside the cave. At the end of each year's sampling period, all salamanders were released at their capture site. To delimit body size cohorts and newborns, the population structure was decomposed by means of FiSAT software (Gaynilo et al., 1996). Male, female and newborn abundances were estimated separately using the generalized removal model  $M_{bh}$  of CAPTURE software that allows for heterogeneity in CP

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**Table 1.** Capture statistics, estimated by temporary removal methods, for *Speleomantes strinatii* age and sex groups. SD = standard deviation of the mean.

Group	Sampled years	Mean estimated abundance ± SD	Mean capture probabilities ± SD
Newborn juveniles	12	27.92±12.82	0.62±0.19
First year juveniles	12	15.75±11.88	0.72±0.18
Subadults	12	19.50±6.33	0.72±0.16
Females	12	17.58±4.60	0.69±0.11
Males	12	23.50±5.60	0.72±0.09
Total population	12	105.00±24.24	0.64±0.07

(White et al., 1982). Square-root-transformed CPs were analysed by repeated measures analysis of variance (RM ANOVA) with year as the fixed and group as the random factor. In accordance with Wilson & Hardy (2002), adult sex ratio was expressed as the proportion of estimated mature males: males/(males + females). Departures from equality were assessed by binomial tests (Wilson & Hardy, 2002). The 95% confidence intervals of the mean sex ratio were obtained by bootstrapping, and the temporal trend of adult sex ratio and the regression slope between sex ratio and newborn abundance were tested by randomization tests with 1000 replicates. Statistical analyses were performed with MINITAB 13.0 and with dedicated macros (Butler et al., 2003).

The capture statistics for the different age and sex classes of *S. strinatii* are presented in Table 1. Overall, CPs were  $\geq 0.60$  and there were no significant differences among groups (RM ANOVA,  $F=1.17$ ,  $df=4$ ,  $P=0.335$ ) and years ( $F=1.07$ ,  $df=11$ ,  $P=0.405$ ). Females and males had high CP and after three removals a large part of the adult population was captured each year. Thus, the estimated abundances of males and females were highly reliable and yielded accurate sex ratio values.

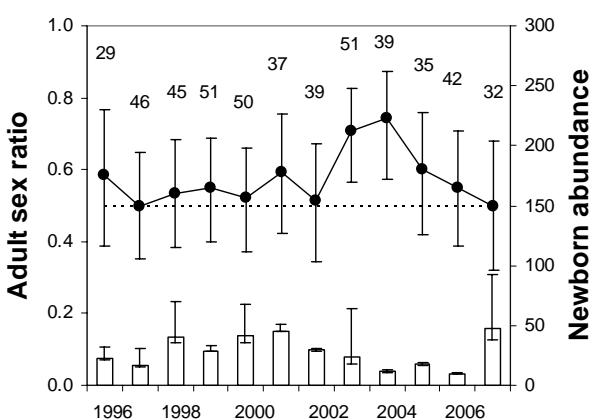
There was no population size effect on ASR ( $r=0.013$ , two-sided randomization test,  $P=0.97$ ; Fig. 1). The mean ASR (0.57) was male biased, with bootstrap 95% confidence intervals (0.53–0.65) which did not include the 0.50 value corresponding to equality between sexes. However, only in two years the excess of males was significant according to binomial 95% confidence limits (see Fig. 1). The 12-year ASR variability was moderate (coefficient of variation = 0.14) and did not show any temporal trend (two-sided randomization run test,  $P=0.88$ ).

There was a significant negative relationship between the ASR and the estimated number of newborn juveniles that were recruited into the salamander population in the following year (Fig. 2,  $r=-0.64$ , estimated slope =  $-109.18 \pm 43.19$  SE,  $t=-2.54$ , two-sided randomization test for slope  $P=0.02$ ).

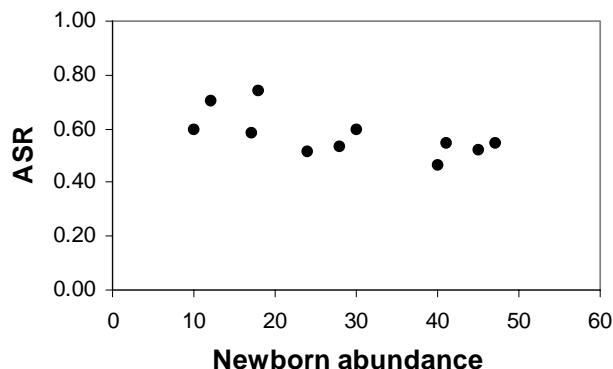
This study suggests that long-term demographic studies may be particularly useful in estimating the ASR in populations in which small deviations from an equal proportion of reproductive adults are found. Indeed, only two out of 12 ASR values were significantly male-biased, thus hindering a correct interpretation of the overall ASR if only a few years were considered. The constancy and

low variability in the ASR values observed during the 12-year study may also indicate that demographic stochasticity was not responsible for the result. A male-biased ASR appears to be a general pattern in many bird species in which a balanced offspring sex ratio and a higher female mortality are well documented (Donald, 2007). In the present case, the constant excess of adult males could be caused by delayed maturity of females, which enter the reproductive population one year later than males (Salvidio, 1993). However, for species with high survival, a small difference between survival of males and females may produce important effects on population adult sex ratio, masking possible effects of differential age at sexual maturity (Girondot & Pieau, 1993). Indeed, higher death rates of breeding females have been suggested to explain the male-biased ASR in some *Desmognathus* species (Organ, 1961). That males tended to survive longer than females was in fact documented in three species of *Desmognathus* by skeletochronology (Bruce et al., 2002), but conversely Leclair et al. (2006) did not find any significant difference in longevity between sexes in four populations of *Plethodon cinereus*. Unfortunately, age and sex survival estimates are completely lacking in *Speleomantes* and thus it is not possible to favour one of these two non-mutually exclusive explanations of the observed male-biased ASR (i.e. males becoming reproductive at a younger age and females exhibiting higher death or emigration rates).

Another remarkable result was the negative relationship between the ASR in one year and the number of juveniles recruited in the population in the successive one. This regulation mechanism suggests that when adult males are overabundant, recruitment of juveniles may be depressed, possibly by intraspecific competition or interference between males and gravid females. In the study population there is no spatial segregation between adult males and females (Salvidio & Pastorino, 2002), thus competition or interference could involve food resources rather than space. Indeed, high trophic niche overlap between the sexes was demonstrated in *S. strinatii* (Salvidio



**Fig. 1.** Adult sex ratio (circles) and estimated abundance of newborn juveniles (histograms) with 95% confidence intervals. The dotted line indicates equal proportions of males and females. Numbers above circles are estimated total adult populations per year.



**Fig. 2.** Relationship between adult sex ratio (ASR) and the estimated abundance of newborn salamanders in the following year;  $r = -0.64$ , two-sided randomization test for slope  $P=0.02$ .

et al., 1994) and *S. italicus* (Vignoli et al., 2006). Thus, if fecundity is related to food availability in female *Speleomantes*, in years when males are over-abundant gravid females may have access to a lower amount of trophic resources and may decrease their egg output and, as a consequence, newborn recruitment.

**Acknowledgements.** The Italian Ministry of Environment, MATTM, issued capture permits (DPN-2007-0010584 for 2007). Thanks are due to the Speleological Group “A. Issel” for allowing access to the study site. The comments of two anonymous reviewers improved the manuscript.

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Accepted: 16 April 2008