Volume 8, Number 2

April 1998

ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL

Published by the
BRITISH HERPETOLOGICAL SOCIETY

Indexed in
Current Contents

HERPETOLOGICAL JOURNAL, Vol. 8, pp. 93-98 (1998)

REPRODUCTIVE DYNAMICS OF A POPULATION OF SMALL MARBLED NEWTS (*TRITURUS MARMORATUS PYGMAEUS*) IN SOUTH-WESTERN SPAIN.

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A breeding population of small marbled newts in a temporary pond in SW Spain was sampled over five successive years. Males and females entered the pond just after it flooded in autumn. The adult aquatic season persisted until March or April, with maximum capture rates occurring mostly in January. Several sampling methods were used of which the most efficient was funnel trapping. Recapture rates were low. The population was estimated at about 1000 newts in 1987. Sex ratio did not differ from 1:1 in three seasons. In the other two seasons, which were characterized by low autumn rainfall, males outnumbered females by 2:1, probably as a result of many females failing to enter the pond to breed in those years. In the last two study years, the mean body size of newts was smaller than in previous years, possibly as a consequence of the adverse conditions of the two preceding autumns, which would have had repercussions for the growth of juveniles. An increase in physical condition and individual body mass throughout the aquatic season was observed in both sexes, confirming that the adult aquatic phase is advantageous for growth and maintenance of newts, as well as being necessary for reproduction. The age structure of the population was obtained in one of the seasons. Most males and females were 2-3 years old and a small percentage was one year old. The frequency of 1 year old mature females was lower than that of males. Females showed higher survival rates than males.

INTRODUCTION

Marbled newts show wide variation in body size throughout their range, with populations consisting of small-bodied newts included in a subspecies (*Triturus marmoratus pygmaeus*). This subspecies has recently been extended to include newts from the mid-southern Iberian peninsula (Garcia Paris, Herrero, Martín, Dorda, Esteban & Arano, 1993). Caetano & Castanet (1993) documented variability in growth and longevity in this species and emphasized that more information is needed on geographic variation in the active season of different populations. Diaz-Paniagua, Mateo & Andreu (1996) found that marbled newts from Doñana, Spain, differ from nearby populations in their small body size and earlier age at maturity, which is mainly due to the short juvenile terrestrial phase.

Similarly, geographic variation has been documented for other *Triturus* species, such as *Triturus vulgaris*, which varies in adult size and life history traits across its range (Griffiths, 1984; Verrell & Halliday, 1985*a*; Accordi, Massarek & Nobili, 1990; Fasola & Canova, 1992). In this species southern populations characteristically have a shorter aquatic period and smaller body sizes (Accordi *et al.*, 1990).

The aim of this study was to document aspects of the reproductive biology of *Triturus marmoratus pygmaeus* in Doñana National Park, showing the intra- and inter-annual variation in sex ratio, abundance, body size and mass of newts during a five year period.

METHODS

Newts were sampled at a temporary pond in Doñana National Park, a sandy area in south-western Spain between the Atlantic Ocean and the marshes at the mouth of the Guadalquivir River (see detailed description in Diaz-Paniagua, 1990). The pond is usually flooded by autumnal rains and lasts until the summer, which is typically dry and hot in the area. During the newt's aquatic season, the estimated area of the pond ranged from about 60 m^2 in December 1986 to approximately 880 m^2 in February 1988, while maximum depth ranged from 16 cm to 120 cm. The vegetation within the pond was mainly composed of meadow herbs on the shores (*Chaetopogon fasciculatus*, *Cynodon dactylon*, *Mentha pulegium*, *Hypericum elodes*, *Juncus heterophyllus* and *Eleocharis multicaulis*) and the hydrophytes (*Callitriche* spp., *Ranunculus peltatus*, *Myriophyllum alterniflorum*) in the deepest areas of the pond. Newts were captured during five successive years (November 1983–April 1988) using different sampling methods. In the first year, newts were captured by dip-netting during the day until no more animals were captured. From November 1984 I also captured newts by hand during the night.

From November 1986, funnel traps were employed following the description in Griffiths (1985) and these were checked three times a night. This method increased the number of newts captured. Each year the pond was sampled once or twice a month from immediately after it formed until no more newts were captured.

All newts captured were measured to the nearest 0.5mm and weighed to the nearest 0.1 g. Body size was estimated from the tip of the snout to the anterior tip of the vent in order to exclude the variation in vent length due to sex and reproductive stage.

Each newt was marked by clipping the longest toe of the right forelimb. The toes were preserved in alcohol for age determination by skeletochronological techniques (see Díaz-Paniagua *et al.*, 1996). The dorsal pattern was photographed and used for individual identification of toe-clipped newts. Additional information was recorded on the development of the crest in males and on the observation of yolked eggs, clearly visible through the abdominal wall of females.

Because of the low recapture rates, population estimates were only calculated from the sample with the highest capture and recapture rates (February 1987). The number of individuals (N_B) and its standard error (SE) was estimated by the Petersen index, with Bailey's modification:

$$N_B = r(n+1)/m+1$$
$$SE = (r^2(n+1)(n-m)/(m+1)^2(m+2))^{1/2}$$

where r = number of animals caught, marked and released the first day; n = total number of animals captured the second day; and m = number of marked newts captured the second day (Donnelly & Guyer, 1994). The age of newts was estimated for 130 males and 54 females from the sampling period of 1986-87, and for 24 males and 10 females from 1985-86.

Survivorship was calculated from the age structure of the population sampled in 1986-87. Due to the lower frequency of individuals of the one-year class, adult survival was only considered for individuals older than two years, the age at which most individuals mature. Survivorship (l_x) was calculated as the ratio of the number of individuals in age class x to the number of individuals in the youngest age class (Krebs, 1994).

ANOVA was used for comparisons of body length, mass and physical condition of newts. In order to avoid pseudoreplication, all data for recaptured newts were excluded from these comparisons.

RESULTS

THE AQUATIC SEASON

In the study area, the annual aquatic season of marbled newts starts once the pond is flooded, and therefore depends on the autumnal rainfall (Díaz-Paniagua, 1992). In Doñana, the heaviest rains normally fall from October to December, as occurred in 1983, 1984 and 1987. However, in 1985 and 1986 rainfall was low during the autumn, but higher during the next winter and spring (Fig. 1). In 1983 and 1984 the newts first entered the pond in November, while in 1985 they did not enter until December. In 1986 the newts arrived in November, and in 1987 in October. The end of the aquatic season normally occurred in March or early April (Fig. 1), although the pond persisted until June or July. Except for three juveniles, all newts captured in the pond during the study period were adults.

NUMBER OF INDIVIDUALS IN THE POND

The number of different newts captured varied depending on the sampling method and ranged from 65 in 1983-84 to 390 in 1986-87, and the total captures ranged from 70 to 571 (Table 1). However, the rise in

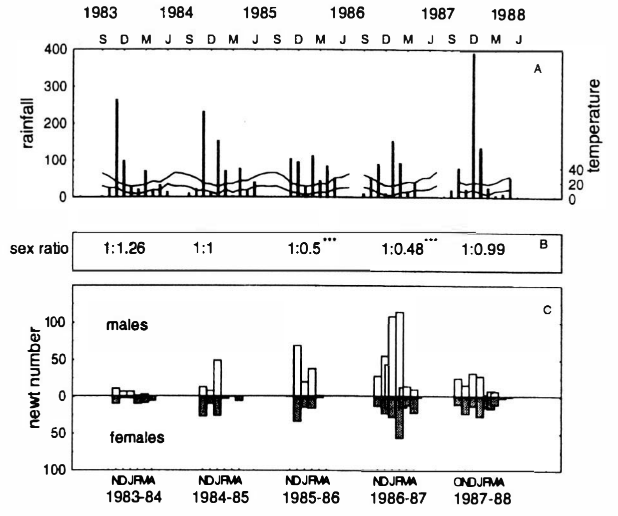

FIG. 1. Variation in (a) monthly rainfall (bars, in mm), and minimum and maximum monthly temperatures (lines, in °C) in the study area; (b) sex-ratio (males:females); and (c) the number of newts captured in the pond in each aquatic season (months are abbreviated by their initials). *** $P<0.0005$, after χ^2).

the number of newts observed in 1986-87 was not due to the greater efficiency of the sampling method alone, as twice as many newts were captured than in the following year using the same method. Within each annual aquatic season, the number of newts gradually increased from the onset to a peak in January. By March or April only a small number of individuals was observed (Fig. 1). The maximum length of stay in the pond based on recaptures was 138 days for a male (November 1986 to April 1987), and 112 days for a female (December 1986 to March 1987).

Recaptures from subsequent years were difficult to detect since newts normally regenerated toes and could only be identified by dorsal patterns. Nevertheless, 28 females and 34 males were recaptured in two consecutive years, and five males were caught in three successive years. Nine females and six males were recaptured in alternate breeding seasons.

The estimated number of newts in the pond in February 1987 reached values as high as 530.8 males (SE=194.0) and 443.3 females (SE=128.6)

TABLE 1. Numbers of different male and female newts captured, and the sampling method used in each annual aquatic season (in parentheses, percentage of recaptures).

Season	Males	Females	Sampling method
83-84	29 (6.5)	36 (7.7)	dip-netting
84-85	61 (15.3)	61 (15.3)	dip-netting/ hand capture
85-86	107 (17.1)	44 (33.3)	dip-netting/ hand capture
86-87	259 (32.9)	131(29.2)	funnel traps
87-88	97 (18.5)	91 (23.5)	funnel traps

SEX RATIO

Males and females entered the pond from the beginning of the aquatic season. Males were twice as numerous as females in the earliest samples of most years, except for November 1984, when females outnumbered males, and November 1983 when the sex ratio was equal (Fig. 1). Males were more numerous than females in the peak sample of all the study years, which (except in 1983-84 and 1985-86) normally occurred in January or February. Females were usually more abundant than males towards the end of the aquatic season (Fig. 1).

The overall sex ratio did not differ from 1:1 in 1984-85, 1985-86 and 1987-88. In contrast, in those years with lower autumnal rainfall, males significantly outnumbered females ($\chi^2_{1985\text{-}86}$=20.35, P< 0.0005; $\chi^2_{1986\text{-}87}$= 70.75, P<0.0005; Fig. 1). The different sampling methods employed during the study period could have influenced results on sex-ratio, if any of them would have favoured the capture of one sex. However, similar male and female recapture rates in dip-netting sampling (Table 1) suggested similar catchability for both sexes.

The same pattern is suggested by the other sampling methods, since the deviation was not always observed in favour of the same sex.

VARIATION IN POPULATION CHARACTERISTICS

Body size. In males, significant differences were detected between the years. These were mainly due to the smaller body sizes of male newts in the last two seasons (Fig. 2; ANOVA: $F_{4,494}$= 88.21, P<0.0005). However, significant variation in the distribution of body sizes within each annual aquatic season was only detected in 1984-85 (ANOVA: $F_{3,62}$= 2.98, P=0.038). In females, significant differences were detected between years for body size (ANOVA: $F_{4,310}$= 23.46, P<0.0005); the female population also showed lower mean body sizes in 1986-87 and 1987-88. A wide range of body sizes was observed in 1986-87 and 1987-88, while from 1983-84 to 1985-86 mostly large individuals were observed. Significant variation in body size of females during the aquatic season was observed only in 1986-87 (ANOVA: $F_{7,110}$= 2.25; P = 0.036).

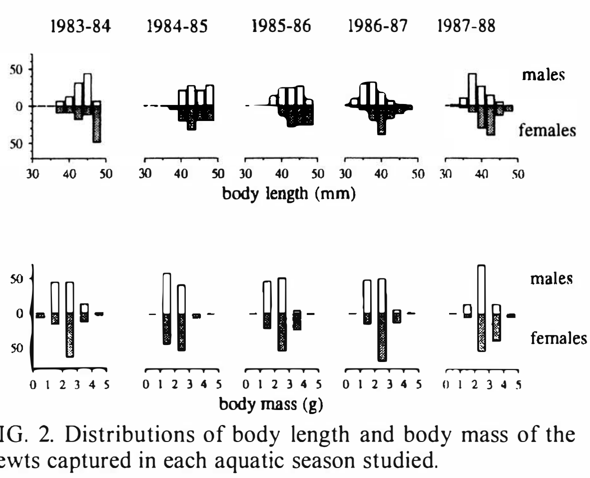

FIG. 2. Distributions of body length and body mass of the newts captured in each aquatic season studied.

Body mass and physical condition. The distribution of male and female body mass in the five study seasons is also given in Fig. 2. Despite the fact that individuals in the pond were smaller in the last two years, they showed heavier body mass than in previous years (ANOVA: males: $F_{4,500}$= 4.36, P = 0.0018; females: $F_{4,323}$= 6.52, P<0.0005). Body mass (BM) showed a significant correlation with body length (BL) cubed (males: BM = 0.707+0.0003 BL^3, R^2= 0.543, females: BM = 0.706+0.0003BL^3, R^2= 0.496) and therefore the ratio (BM / (BL^3))·1000 was used to analyse the variation in physical condition of newts within the aquatic season. Significant differences were observed between the years (ANOVA, males: $F_{4,492}$= 128.21, P< 0.0005; females: $F_{4,310}$= 55.5, P< 0.0005), but not between males and females (ANOVA: $F_{2,813}$= 3.10, P = 0.078).

There was intraseasonal variation in the last two study years because of the large number of individuals recorded. Females started both seasons with lower index values than males, although both sexes showed a general increase. A decrease in physical condition of males and females was observed in the later samples of both years, coinciding with a decrease in the number of individuals in the pond and with the end of egg laying by many females. In general, males and females finished the aquatic season in a better physical condition than at the onset (Fig. 3).

Recapture data showed an increase in body mass in most individuals throughout the aquatic season. However, weight loss occurred in a few newts that were observed at the end of one season and then recaptured at the start of the next. Data for some males indicated a small or zero weight gain during the first days of the season, yet a large increase later on. Females usually increased weight from the first days onwards (Fig. 4).

Reproductive stage. Females had large eggs in the abdominal cavity from the second sampling period onwards, with a peak of oviposition in January and February, when 100% of females contained large yolked eggs. High percentages of such ovipositing females persisted until March, when only a small number of females were caught.

In 1987-88, males with high dorsal crests were observed from October to February, while low-crested males were detected only at the beginning and at the end of the season. However, during the previous year, 1986-87, when twice as many individuals were caught, males with low crests were observed during the whole

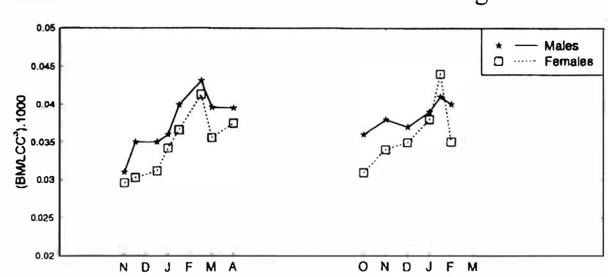

FIG. 3. Variation in the male and female mean physical condition through the last two aquatic seasons studied, 1986-87 and 1987-88.

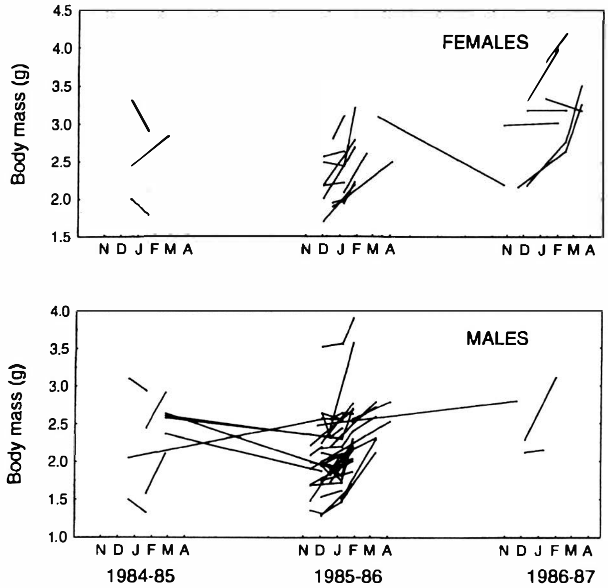

FIG. 4. Variation in body mass of the individuals recaptured during three consecutive aquatic periods.

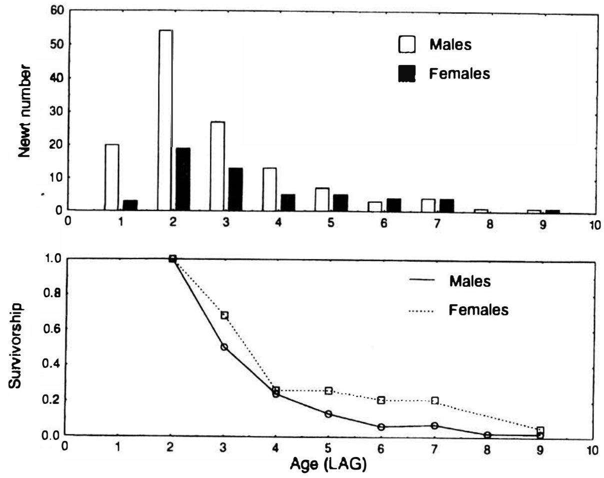

FIG. 5. Age structure and survival rate of male and female populations in 1986-87. LAG = lines of arrested growth in phalange sections of newts.

season, making up about 30% of the males in December and February, and 65% in January.

Age and survivorship. In a previous study we observed that most marbled newts from Doñana matured at two years, with a smaller number maturing at the age of one year (Díaz-Paniagua *et al.*, 1996). In 1986-87, 15 % of adult males were one year old, while 60 % were 2-3 years old (Fig. 5). Only 5.6% of the female population were one year old individuals, while about 50% were 2-3 years old (Fig. 5). The age of another 24 males and 10 females was estimated for the 1985-86 population, when 12.5% of males were one-year old, and all females were older than two years.

Although 10 year old females were detected in the previous study (Díaz-Paniagua *et al.*, 1996), the maximum longevity detected in 1986-87 was 9 years in both sexes. From the age structure of this season, females showed higher survival rates than males, since there were higher proportions of females than males more than two years old (Fig. 5).

DISCUSSION

Pond flooding marks the end of Doñana's marbled newts annual inactive period during the hot and dry summer months. The unpredictability of flooding confers a characteristic inter-annual variation to the onset of the newt aquatic season. In contrast, there is no flexibility at the end of the season. Although the pond normally lasted up to June or July, the last newts were commonly found in March, or rarely, in April when the first larvae hatch (Díaz-Paniagua, 1992).

As in other newt species (Verrell & Halliday, 1985*a,b*), the aquatic season should not be considered as just a reproductive season, but also as being important for the maintenance and growth of individuals. Although mating and oviposition are important activities, they do not cover the entire aquatic period, in which a substantial increase in body length (Díaz-Paniagua *et al.*, 1996) and mass occurs for both sexes. In other studies of newt populations, substantial weight loss occurred throughout the aquatic season (Harrison, Gittins & Slater, 1983; Andreone & Giacoma, 1989). The benefit obtained during this season probably depends on the productivity and duration of the breeding habitats, which may sometimes be adverse and uncertain. The newt population in Doñana is at the southern limit of the range of the species, where small size and early age at maturity may be adaptations to a highly unpredictable environment (Begon & Mortimer, 1986). The dry and hot summer conditions in this area are likely to constrain the annual activity period of newts to the aquatic season, when, together with their reproductive effort, other activities must be important for survival and growth of individuals. Northern populations of *T. m. marmoratus* are probably constrained by lower winter temperatures, as they breed later in the year in northern Spain, from February to May (Braña, 1980; Salvador, Alvarez & García, 1986). At the northern limits of the species range, marbled newts stay in ponds from March to June (Bouton, 1986). Southern Portuguese newts have an aquatic season similar to that of newts from Doñana (Caetano & Castanet, 1993). However, compared to the Doñana population, the Portuguese newts attain maturity at a later age and are characterized by larger body size and greater longevity (see Díaz-Paniagua *et al.*, 1996).

Males and females seem to have different dynamics, considering the wide within-year and between-year differences observed in sex ratio, and their different survival rates and age structures. Both sexes entered the pond at similar times, and individuals may persist there for a long time. Residency in the pond is longer than that detected for a population of *T. m. marmoratus* in northern Spain where maximum residence of adult newts in a pond was 56 days (Salvador *et al.*, 1986). Fasola & Canova (1992) found wide variation in the annual period of residence in water among three species of *Triturus* coexisting in the same pond. The species with shorter residence used the pond exclusively for reproduction, while the other species persisted in the pond after reproduction, when newts could perform other activities which would favour growth. Verrell & Halliday (1985*a*), studying a population of *T. vulgaris*, reported that body mass declined over most of the aquatic season, and only increased in those newts that remained in the pond after breeding. In Doñana, most newts gained weight as soon as they entered the water, and the gradual increase in overall physical condition revealed that the aquatic season was advantageous for both sexes. The highest male reproductive effort takes place early in the season, after they have developed their crests, while during the late season they are probably mainly devoted to feeding and growth. Females, however, make an important investment in reproduction over a longer period. From an early stage in the active season they initiate the process of egg yolking and make a great investment later in the season during egg-laying, with the peak of oviposition being in February. Up to this time females showed a notable weight gain, and became extremely voracious. Although egg deposition must represent a great effort and a considerable weight loss, they finished the aquatic season in better condition than at the onset of the season.

A wide range of variation in sex ratios has been observed for other *Triturus* populations during the aquatic season, with an excess of males (Hagström, 1979; Harrison *et al.*, 1983; Griffiths, 1984; Andreone & Giacoma, 1989), equality (Verrell & Halliday, 1985*b*), and an excess of females (Bell, 1977; Verrell & Halliday, 1985*a*; Salvador *et al.*, 1986). The skewed sex ratio was explained in *T. vulgaris* populations by a differential mortality of individuals of one sex because of their greater reproductive effort (Bell, 1979; Harrison *et al.*, 1983), which was supported in one of these populations by the observation that females lost weight during the breeding season. In the present study, equality was observed in most of the years, but in those seasons of lower autumnal rainfall, males were twice as abundant as females. The age structure in one of these years (1986-87) revealed a higher proportion of young males than of females, while in the smaller sample of 1987-88, when the sex ratio was also skewed, all females were older than two years, and 12.5% of males were one year old. This certainly contributed to the unequal sex ratio.

The early months of the season, when females are replenishing their physical condition and yolking the eggs, must be a requirement for one year old females to initiate breeding, which is thus improbable in seasons with delayed rainfall. The scarcity of resources in autumn may also have negative effects on those older females which could not reach adequate physical condition for oocyte maturation and ovulation. This, in turn, could explain why some females did not reproduce in such years. The lower reproductive frequency of females would also explain the result of the differences in age structure of the sexes, with higher survival rates among females. The recapture data confirm that females may reproduce in two successive years while males were confirmed for three succesive breeding seasons. Accordi *et al.* (1990) also found variation between years in sex ratio in a southern population of *Triturus vulgaris*, because not all females entered the pond in dry years. Griffiths (1984) commented on the possibility of non-annual breeding of a proportion of females in an English population of *T. vulgaris*. In Doñana, during a drought which lasted from 1991 to 1994, I observed an attempt at breeding in January 1994, when the pond studied was ephemerally flooded. The population sample consisted of 23 males and only five females (male:female ratio, 1:0.27), confirming the lower availability of breeding females under suboptimal conditions.

Verrell & Halliday (1985*a*) also found a variation in the operational sex ratio over the breeding season, due to the synchronicity of female ovulation, while males were able to maintain courtship activity and produce spermatophores over a prolonged mating season. A similar variation was observed by Griffiths (1984), who found a slightly male-biased sex ratio in the aquatic population, while females outnumbered males outside the pond. In the present study variation was also observed within most of the seasons. During the first part of the season there were more males than females, while in the second part, females were more numerous, probably because they are obliged to persist in the pond to conclude oviposition.

Despite the low autumn rainfall and the 1985-86 and 1986-87 skewed sex ratio already discussed, the number of captures was high during these periods. However, although abundance cannot be compared in both years because of the different sampling methods employed, high population size was estimated in both periods. In 1987 the population size was estimated to be approximately 1000 individuals and the pond extended over some 540 m^2. This can be regarded as a high density of newts, if compared with other dense newt populations (Glandt, 1982; Verrell & Halliday, 1985*a*; Miaud, 1991). The decrease in abundance detected in 1987-88 could be explained by lower reproductive success of the population in 1985-86, when the skewed sex ratio suggested that an important fraction of the female population did not breed.

The last two seasons studied differed from the previous years in (1) mean body size of newts, which was smaller than in previous years; and (2) a general increase in body mass. The smaller body size could be explained by higher recruitment of young adults from the preceding years; however, the similar proportion of one-year males in 1986-87 and 1985-86 does not support such an idea. Rather, the smaller body size could be a consequence of the seasons of scarce autumn rainfall, with a shorter activity period which could have repercussions on the growth of individuals, in particular those newts which did not breed and juveniles which would mature at the age of one or two years at a smaller body size. An *a posteriori* Duncan Test showed that the overall heavier body mass was significantly different in 1987-88, after a very rainy year, when the size of the pond increased in size and probably in resource availability.

ACKNOWLEDGEMENTS

This study was financially supported by DGICYT (project PB-91-0115-C02-02) and Junta de Andalucía (Grupo RNM 0128). Rosario Rivas encouraged me and assisted in the fieldwork. I thank Claudia Keller and Ana Andreu for their critical reading of the manuscript; and T. R. Halliday, J. W. Petranka, M. Sparreboom and B. Arano, for their comments.

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Accepted: 5.6.97