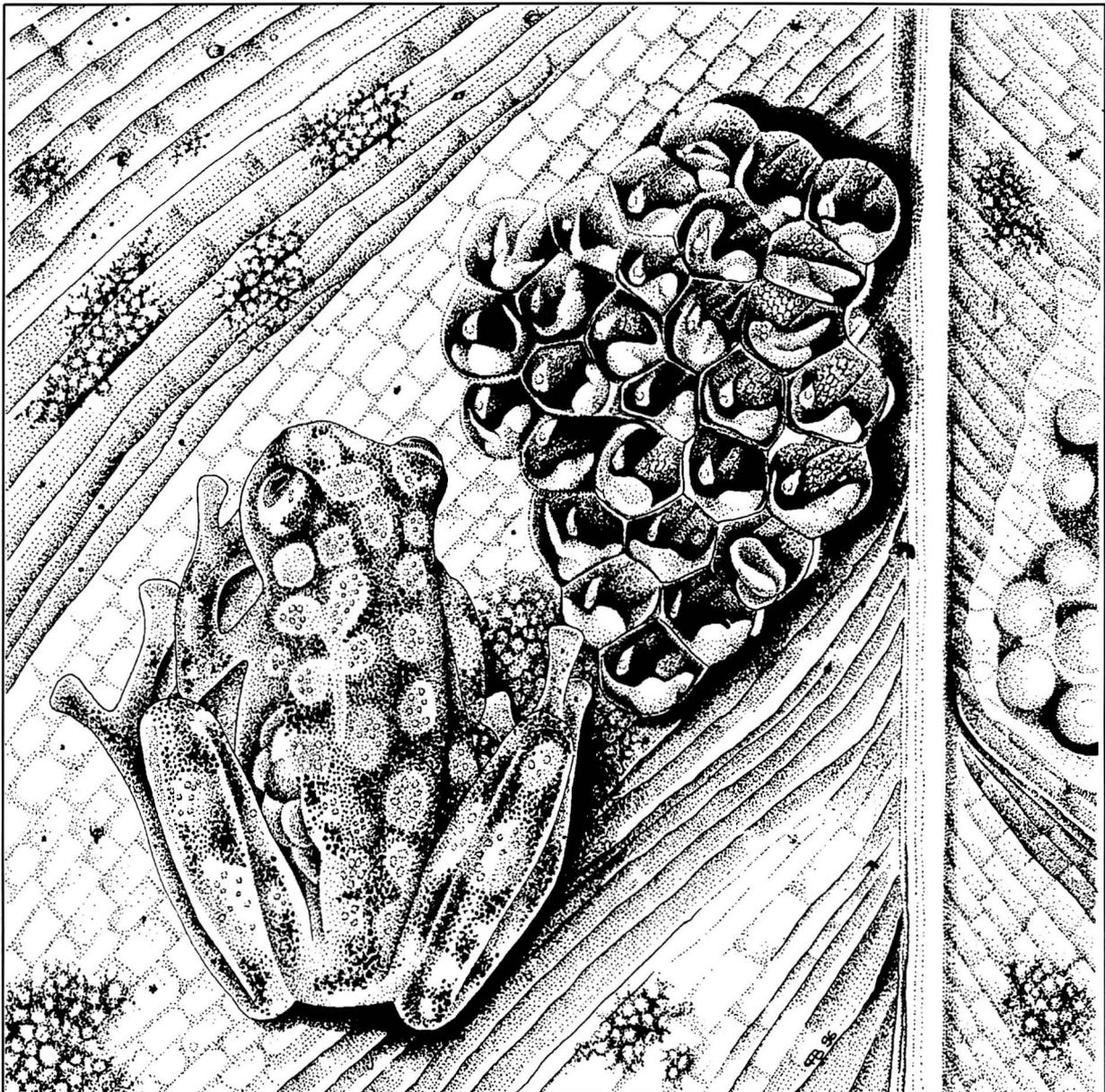


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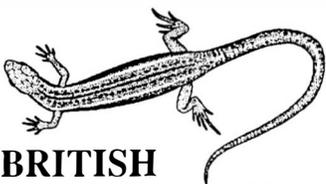
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FRONT COVER: Glass frog, *Centrolenella* sp. with eggs (P. Benson)

## BEHAVIOURAL INTERACTIONS BETWEEN A RARE MALE PHENOTYPE AND FEMALE UNISEXUAL *LEPIDODACTYLUS LUGUBRIS*

SUSAN G. BROWN AND SUSAN MURPHY-WALKER

*Social Sciences Division, University of Hawaii at Hilo, Hilo, Hawaii, 96720-4091, USA*

A rare male phenotype of the unisexual gecko, *Lepidodactylus lugubris*, was captured on the University of Hawaii, Hilo campus. The male was housed with females in different stages of their reproductive cycles. Observations were made of interactions between the male and individual females. The male approached females with either no evidence of egg development or small, probably ovarian, eggs more often than females with larger, probably oviductal, eggs; and was observed neck-biting and moving on top of females although no intromissions or copulations were observed. Female geckos were more aggressive than the male; the male was less likely to approach females that reacted to his approaches aggressively. Although it seemed that the male was attempting to court the female geckos, we do not know if courtship attempts failed because of the male or female behaviour. Sperm were present in the testes and epididymis. However, all motile sperm appeared to be headless, suggesting that the male was infertile.

### INTRODUCTION

Unisexual species have been documented in many lizard genera (*Cnemidophorus*, *Lacerta*, *Lepidophyma*, *Hemidactylus* and *Lepidodactylus*) and in one species of snake (*Ramphotyphlops braminus*; Nussbaum, 1980). Most, if not all, of the unisexual reptiles arise from the hybridization of two sexual ancestors (Cole, 1990) and subsequently reproduce through premeiotic doubling of their chromosomes, which results in a full chromosome complement after meiosis (Cole, 1975). The genotypes of the unisexual hybrids are thus maintained intact except for later mutations. It is surprising, then, when one encounters a phenotypic male individual in the midst of a unisexual clone (for example see Ota *et al.*, 1993).

Male phenotypes are found in unisexual lizard species under a variety of conditions. When the range of a unisexual species overlaps with the range of a congeneric sexual species, the unisexuals are often found with bite marks on their abdomens indicating that mating has occurred (Darevsky & Danielyan, 1968). In some cases of unisexual-bisexual mating, hybrid male young are produced by the unisexual female. For example, male hybrids resulted from the mating of the unisexual whiptailed lizard, *Cnemidophorus uniparens*, with the sexual species, *C. inornatus*; from the unisexual *C. neomexicanus* with the bisexual *C. inornatus* (Cuellar & McKinney, 1976); and from the unisexual *C. laredoensis* with the bisexual *C. gularis* (Walker *et al.*, 1989). Hybrid males have also been reported in the unisexual *Lacerta* (as cited in Darevsky *et al.*, 1978).

Phenotypic males have also been found among offspring of unmated unisexual lizards. For example, Darevsky *et al.* (1985) reported a number of lethal abnormalities in the offspring of unmated unisexual

*Lacerta*. Most of the abnormal embryos of the unisexual species (*L. armeniaca*, *L. dahli* and *L. rostombekovi*) had hemipenes. The majority of the male foetuses died during embryogenesis, and foetuses that were extracted from eggs died within a few days. Adult males have been found in collections of unisexuals obtained in areas where the range of the unisexual did not overlap with the range of a congeneric bisexual species, indicating that some non-hybridized unisexual males survived to adulthood. Males were found in three unisexual species of *Cnemidophorus* (*C. tesselaus*, *C. exsanguis* and *C. velox*; Taylor *et al.*, 1967), in *Lacerta* (*L. armeniaca*; Darevsky *et al.*, 1978) and in a unisexual gecko (*Lepidodactylus lugubris*; Cuellar & Kluge, 1972). To the best of our knowledge, the behaviour of a phenotypic male unisexual has yet to be described.

The courtship and copulatory behaviour of geckos is not well documented. Courtship behaviour in the diurnal banded gecko consists of tail waving, licking and bites to the female's body, followed by a strutting walk in which the male pushes the female forward. During copulation, the male grasps the female by the neck and then intromits (Porter, 1972). Mating behaviour is rarely observed in nocturnal geckos. Church (1962) observed only four matings between *Hemidactylus frenatus* pairs during a year of study and six years of living with the geckos. Male *H. frenatus* apparently engage in little or no courtship behaviour. The males stealthily approach the female, rush at her and then copulate (Marcellini, 1977a). No data on mating and copulatory behaviour in sexual *Lepidodactylus* are available. Despite the paucity of data on mating behaviour in nocturnal geckos, the present study was designed to (1) document and describe any mating attempts between a phenotypic male and female *L. lugubris*; and (2) compare the interactions between

male and female *L. lugubris* with the interactions previously described between female *L. lugubris* (Brown *et al.*, 1991).

## METHODS

### SUBJECTS

Seven *L. lugubris* were collected in the grounds of the University of Hawaii, Hilo campus. One gecko was a male phenotype captured on 22 May 1986 (confirmed *L. lugubris* in Radtkey *et al.*, 1995). The male phenotype had well-developed hemipenial sacs and femoral pores. When the male was dissected (12 June 1990), he was at least five years old, as he was captured as an adult and it requires 9-12 months for a gecko to reach maturity (Brown & O'Brien, 1993). The contents of the epididymis and vas deferens were squeezed out and placed in amphibian ringers solution. Sperm were examined for evidence of motility using a phase-contrast microscope. The testes were removed and fixed in Steives fixative (Humason, 1979) for 24 hr. The samples were then washed in 50% ethanol for 30 min, post-treated in iodine-alcohol solution for 6 hr, and were embedded in Paraplast-Plus. Sections of 7-10 $\mu$  in thickness were stained with either Delafield's Hematoxylin and Eosin Y (H&E, regressive method) or Feulgen's technique (Humason, 1979) and examined for histological information regarding sperm formation and maturation.

All six females had produced at least one egg clutch prior to placement with the male. The females were in different phases of their reproductive cycles when individually housed with the male. Reproductive phase was determined in two ways: (1) time elapsed since oviposition, and (2) visible presence of ovarian or oviductal eggs. Eggs were measured by placing the gecko in a narrow plexiglas box and examining the gecko's translucent ventral surface. Eggs greater than 1 mm in size can be observed in this manner. Two of the females had no visible signs of egg development; one was housed with the male immediately after oviposition (F-OVI) and the other a week after oviposition (F-OVI-1WK). The remaining four geckos had visible eggs measuring 3 mm (F-3MM), 5 mm (F-5MM), 7 mm (F-7MM) or 9 mm (F-9MM). F-9MM laid eggs while housed with the male.

### PROCEDURE

The study was conducted from 28 October 1986 to 5 March 1987. Each female was individually housed with the male for five days in a 32 cm x 28 cm x 31 cm plexiglas enclosure. Enclosures contained a wooden platform suitable for hiding, a plant, and an inch of pebbles covered with sphagnum moss. An interval of at least 10 days occurred between each time the male was housed with a female. Observations began 4 hr after pairing and were made during the morning (0600 - 1200 hr) and afternoon (1200 - 2100 hr). A total of 51.25 hr of observations were made, 27.75 hr in the

morning and 23.5 hr in the afternoon. All behaviour that occurred between the male and each female was recorded in a series of 15 min serial records. At least six serial records were obtained (three in the morning and three in the afternoon) daily. The total numbers of serial records collected per pair was as follows: F-OVI = 30; F-OVI-1WK = 41; F-3MM = 33; F-5MM = 34; F-7MM = 33; F-9MM = 34. The following interactive behaviour patterns were recorded during the observations: *orient to*, *face to*, *approach*, *orient away*, *face away*, *move away*, *click*, *push-up*, *lunge*, *bite*, *touch*, *in proximity* as defined in Brown *et al.* (1991), and *follow*, *head-bob*, *hit*, *on top of*, *chirp* and *multiple chirp*, all behaviours which we had not previously observed in *L. lugubris* and which are defined in Table 1.

### ANALYSIS OF RESULTS

Interactive behaviour displayed by the male and females were grouped as follows: behaviour associated with contacting included *orient to*, *face to*, *approach* and *follow*, and behaviour associated with withdrawal included *orient away*, *face away* and *move away*. Aggressive behaviour was divided into three categories: *clicks*, *head-bobs/pushups* and *lunges/bites/rurrs*. Mean frequencies per 15 min were obtained for each male/female pairing, and grand means were then computed across all pairings. Wilcoxon tests for related samples were used to compare male and female behaviour.

To analyse changes in interactive behaviour across time, behaviours were compared across the first four 24 hr intervals of collected observations. Friedman tests for dependent samples were used to analyse behavioural changes over time.

TABLE 1. Definitions of previously undescribed interactive behaviours observed between the male and female geckos.

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*Follow:*

Gecko moves after another as it moves away.

*Head-bob:*

Gecko moves head up and down; the rest of its body remains stationary.

*Hit:*

Gecko contacts another with front feet.

*On top of:*

One gecko climbs onto another, either remaining there or immediately moving off.

*Chirp:*

Soft slow vocalization only produced by one female.

*Multiple chirp:*

A long extended vocalization only produced by the male.

---

TABLE 2. Summary of male and female interactive behaviour.

Behaviour	Female		Male		<i>U</i>	<i>P</i>
	Grand mean	SD	Grand mean	SD		
<i>Contact</i>	0.6	0.3	0.7	0.6	7.5	NS
<i>Withdrawal</i>	0.4	0.2	0.6	0.4	5.0	NS
<i>Click</i>	3.2	2.1	0.0	--	0.0	<.05
<i>Head-bob/ Push-up</i>	0.4	0.4	0.1	0.1	0.0	<.10
<i>Lunge/Bite/ Rurr</i>	0.5	0.3	0.1	0.1	0.0	<.05

## RESULTS

## MALE BEHAVIOUR

In his interactions with the females, the male displayed more contact and withdrawal behaviour than aggressive behaviour (Table 2). The male *L. lugubris* was more likely to approach females with no sign of egg development or small eggs than females with large eggs ( $r = -0.65$ ; Fig. 1) and to withdraw from these females after the approach ( $r = -0.78$ ; Fig. 1). The male was observed biting females five times. The majority of the time (3/5), the male approached the female, bit her on the neck and then moved away without further interaction. The male was observed on top of a female three times during the study. On two occasions the male was lying on top of F-OVI at the beginning of the 15 min serial record. Once the male remained on F-OVI throughout the record, and once, when the experimenter disturbed the cage, the male moved away. During the above observations, the male neither bit the female nor curled around her. The third time the male moved on top of a female occurred with F-5MM after she approached him while clicking. Once the male moved on top of her, the female became quiet, and the male moved off of her and away.

The male *L. lugubris* vocalized a multiple chirp (MC) call four times (once in the morning and three times in the evening after 1830 hr) with three different females, F-OVI-1WK ( $n = 2$ ), F-5MM ( $n = 1$ ) and F-9MM ( $n = 1$ ) during our observations. While calling, the male was located either in ( $n = 3$ ) or behind the platform ( $n = 1$ ). No interactions between the male and females were in progress at the time of the MC calls. After the MC calls, the females did not approach the male. F-OVI-1WK remained out of the experimenter's sight ( $n = 2$ ), F-9MM continued moving about the enclosure without approaching the male, and F-5MM continued eating a mealworm and chirped softly.

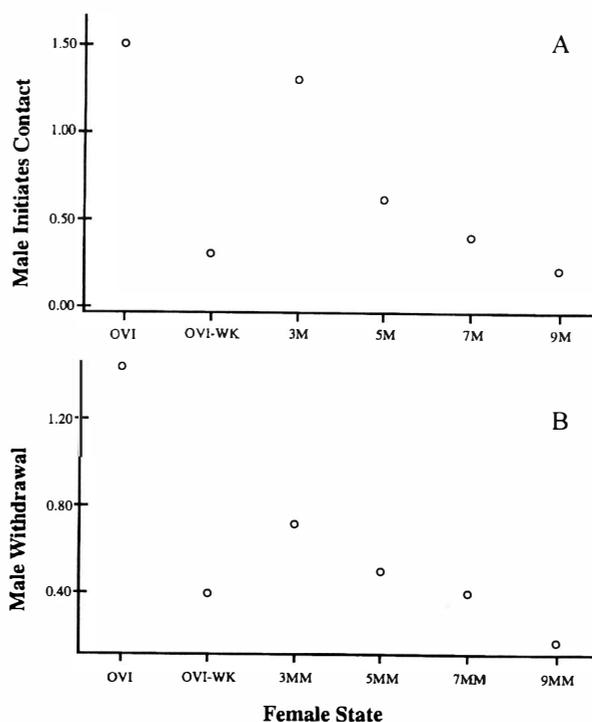


FIG. 1. The relationship between female reproductive state and (A) the male's attempts at contacting the female; and (B) the male's withdrawals from the female. See methods for interpretation of abbreviations for female state.

## FEMALE BEHAVIOUR

Females exhibited higher frequencies of aggressive behaviour (*clicks*, *head-bobs/push-ups*, and *lunges/bites/rurrs*) than the male throughout the observations; the differences were statistically significant (see Table 2). Females responded to male approaches in a variety of ways: by intense aggression (16/67), by moderate aggression (7/67), by moving away (7/67), by orienting to or away from the male, and by not reacting (37/67). Females with small eggs were more likely to react to the male's approach aggressively than females with large eggs ( $r = -0.55$ ). Female bites, unlike male bites, always occurred during prolonged aggressive interactions. F-3MM and F-5MM moved on top of the male during the observations. Usually (7/9 times) the female climbed over or onto the male during an aggressive interaction; twice the female rurred while on top of the male. On two occasions the female climbed over the male and moved to another part of the enclosure.

The male and the females were equally likely to exhibit contact (*orient to*, *face to*, *approach* and *follow*) and withdrawal behaviour (*orient away*, *face away* and *move away*) (Table 2). Behaviours associated with contacting, withdrawing from and maintaining proximity to another animal exhibited no statistical change across time. Neither did behaviour associated with aggression (*clicks*, *head-bobs* and *push-ups*, and *bites*, *lunges* and *rurrs*).

## HISTOLOGICAL DATA

The male *L. lugubris* examined in the present study demonstrated small but apparently normal testes and

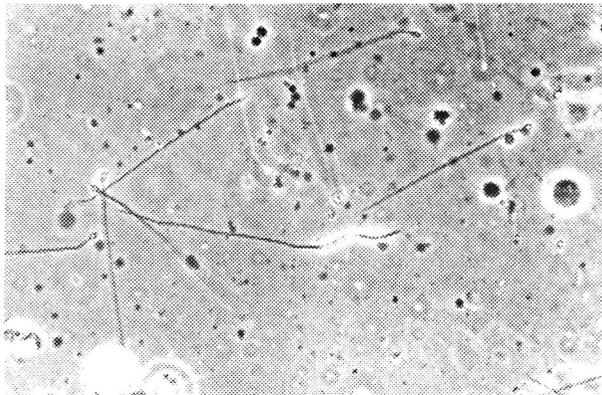


FIG. 2. Motile headless sperm and immotile sperm with head.

sperm ducts. There was an apparent lack of typical cell division events in the testes when compared to a normal adult male *Hemidactylus frenatus* (Murphy-Walker, personal observations). Histological and *in vitro* examination of testicular and epididymal sperm revealed that the majority of sperm present were headless and only headless sperm were motile (Fig. 2).

#### DISCUSSION

The male *L. lugubris* displayed behaviours, such as neck biting and positioning himself on top of a female, associated with gecko courtship (Porter, 1972). We did not, however, observe a completed intromission or a copulation. The male was also more likely to approach females that had recently laid eggs; however, these females responded to male approaches with behaviours most often observed in dominance contests between females (Brown *et al.*, 1991). If the male's behaviours were indeed courtship, then it is possible that either the male and/or the female *L. lugubris* might not possess the behavioural repertoire needed to respond to and complete a normal courtship and mating sequence.

In our previous research on the behaviour of *L. lugubris* (Brown *et al.* 1991), the interactive behaviour between female dyads decreased over time, reflecting a stabilization of the dominance relationships between females. In contrast to our previous research, the frequencies of the interactive behaviours were maintained at high levels throughout the five days the male was housed with each of the females. High levels of interactive behaviours were most likely maintained between the male/female dyads because neither mating nor dominance status was resolved by the end of the five days of observation.

The *L. lugubris* male vocalized the multiple chirp call associated with many gecko species (Marcellini, 1977b). The MC call most likely functions as a territorial spacing mechanism among male geckos. Marcellini (1977b) showed that in the house gecko, *Hemidactylus frenatus*, the call repelled male but was ignored by female *H. frenatus*. Female *L. lugubris* also did not respond to the male's MC calls. The fact that the phenotypic male *L. lugubris* used the MC call indicates that he possessed the ability to display behaviour usually not associated with unisexual geckos.

Even though unisexual species occasionally produce phenotypic males, it is unlikely that the males are capable of reproduction due to abnormalities in spermatogenesis. Of the phenotypic male *L. lugubris* described by Cuellar & Kluge (1972), only one had apparently normal testes and sperm ducts. The male *L. armeniaca* described by Darevsky *et al.* (1978) lacked the typical cell order found in the testes of bisexual *Lacerta* and had few mature sperm. The majority of the male's sperm in the present study were headless and probably incapable of fertilization as there was no apparent nuclear material present for recombination events nor enzymes capable of penetrating egg membranes as evidenced by the lack of an acrosomal cap. Unfortunately the lack of sufficient samples did not allow for discrimination between mitotic, meiotic, or spermatogenic abnormalities as the causal agent of headless sperm.

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## EFFECTS OF TEMPERATURE AND BODY WEIGHT ON GASTRIC EVACUATION RATES OF ALPINE NEWT (*TRITURUS ALPESTRIS*) LARVAE

ROBERT SCHABETSBERGER<sup>1</sup>, SUSANNE BROZEK<sup>1</sup>, KARL ENTACHER<sup>2</sup>,  
CHRISTIAN JERSABEK<sup>1</sup> AND ALFRED GOLDSCHMID<sup>1</sup>

<sup>1</sup>Institute of Zoology, University of Salzburg, Hellbrunnerstrasse 34, A-5020 Salzburg, Austria

<sup>2</sup>Institute of Mathematics, University of Salzburg, Hellbrunnerstrasse 34, A-5020 Salzburg, Austria

We present different polynomial functions to describe gastric evacuation rates of alpine newt larvae in relation to temperature and body dry weight. Gastric evacuation rates increased with increasing temperature and decreased with increasing body weight during early development. Gastric evacuation rates measured in the laboratory were low compared to those estimated under field conditions.

### INTRODUCTION

The driving force behind gastric evacuation studies in fish has been the need to estimate daily food consumption (Bromley, 1994). Elliott & Persson (1978) developed a now widely-used method for calculation of daily food consumption. The Elliott & Persson model, although initially developed for fish, is equally applicable to other poikilothermic vertebrate predators, and it has been used to estimate the feeding rates of alpine newts on zooplankton prey (Schabetsberger & Jersabek, 1995). When urodeles are top predators in lentic communities, they may depress the population size of certain crustacean species (Dodson, 1970). However, their impacts on zooplankton communities seem low relative to those of planktivorous fish (Strohmeier & Crowley, 1989; Holomuzki *et al.*, 1994; Schabetsberger *et al.*, 1995). Knowledge of amounts of food consumed by urodeles during development will be important to understand the role of urodele larvae as a structuring force in fishless lakes and ponds. Yet little information on gastric evacuation rates is available for urodeles (Schabetsberger, 1994). The aim of this paper is to present mathematical functions which allow the calculation of gastric evacuation rates in relation to temperature and body weight. The fits of a linear and two exponential models were compared.

### METHODS

#### EGG COLLECTION AND REARING OF LARVAE

One hundred and twenty adult (60 females, 60 males) newts (*Triturus alpestris*) were collected in mid-June from breeding ponds in the north-eastern calcareous Alps of Austria (Totes Gebirge, 1650 m altitude). In the laboratory groups of six females and six males were kept individually in aquaria (56 x 36 x 10cm), and strips of floating plastic (polyethylene, 30 cm long, 0.8 cm wide) were provided as substrate for oviposition. Newts were held at 20°C under a light:dark cycle of 17:7 hr (light from 0500 hr to 2200 hr) and fed with tubificid worms. Eggs were collected each day and moved to three aerated 200

litre tanks kept at 8°C. On completion of egg collection, adults were returned to breeding ponds. Temperature in the incubation tanks was raised to 22°C within two days and a light:dark cycle of 12:12 hr was imposed (light from 0800 hr to 2000 hr). This regime ensured that most of the larvae hatched within 9-10 days. Developing larvae were fed daily on finely-cut tubificid worms. The worms were active during feeding and triggered prey capture in the newt larvae. Animals in the rearing tanks and those used in the experiments were held at the same temperature regime.

#### FEEDING EXPERIMENTS

During the development of the larval cohort three series of experiments were conducted in turn with different size classes of larvae (small: 1.7-2.2 mg body dry weight; medium: 8.3-13.3 mg; large: 29.3-39.9 mg). For each series the size class was tested consecutively at four experimental temperatures (8, 12, 16 and 20°C, Fig. 1).

Before the start of each series the temperature in the climate chamber was lowered to 8°C within three days (Fig. 1). For each experimental temperature a subset of 150-180 larvae was removed from the tanks and held individually in 50 ml jars to avoid gill damage due to aggressive behaviour of starving conspecifics. The jars were covered with a 1 mm mesh and placed in aerated aquaria (56 x 36 x 10 cm) in the climate chamber. Then the animals were starved for a certain interval to ensure gastric emptying, which was faster than in the subsequent experiments due to less stomach contents of animals in the rearing tanks (small size class at 8, 12, 16 and 20°C for 48 hr; medium size class at 8 and 12°C for 72 hr and at 16 and 20°C for 48 hr; large size class at 8 and 12°C for 96 hr

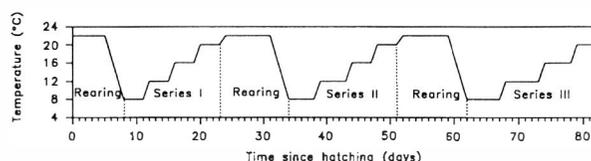


FIG. 1. Diagram of the experimental design.

and at 16 and 20°C for 72 hr). Following food deprivation finely-cut tubificids were provided to the newt larvae for three hours around noon. Food was then removed and thereafter 30 larvae were anaesthetized in MS 222 and fixed in 4% formaldehyde at 3-5.5 hr intervals. Following the feeding experiment at 8°C the next subset of larvae was removed from the rearing tanks and the temperature in the climate chamber was raised to 12°C within 24 hr. The same experimental procedure as described above was then repeated at 12, 16 and 20°C. After finishing a series of experiments the temperature in the climate chamber was raised to 22°C for seven days to get the larvae at larger size (Fig. 1).

Gastric evacuation rates of larvae in the natural habitat were available from a previous study (Schabetsberger, 1994). Briefly, 150 to 200 larvae were collected in an alpine lake during September and October. Food consisted of crustacea and chironomid larvae. Ten to fifteen larvae were placed in food-free cages and exposed in 3 m depth at the lake bottom. Changes in water temperature were within  $\pm 1^\circ\text{C}$ . Every 4 hr 15-30 larvae were then removed, anaesthetized with MS 222 and fixed in 4% formaldehyde. Seven different experiments were conducted at temperatures between 3.9 and 10.6°C. All the larvae used in the experiments would have died in the natural habitat due to anoxic conditions under the ice cover (Jersabek & Schabetsberger, 1996).

After eight weeks in the fixative, stomach contents of five (small and medium sized larvae) or three (large larvae) individuals were pooled, placed in preweighed aluminum boats, dried to constant weight at 60°C (48 to 96 hr) and weighed to the nearest  $\mu\text{g}$ . Larvae were dried and weighed in the same way and stomach contents were expressed as percentage body dry weight.

#### DATA ANALYSIS

*Gastric evacuation rates.* An exponential model of the form:

$$S_t = S_0 e^{-Rt} \quad (1)$$

was fitted to geometric means of stomach contents using a non-linear least squares technique (Marquardt-Levenberg algorithm; Conway, Glass & Wilcox 1970).  $S_t$  is stomach content at time  $t$  (% body dry weight),  $S_0$  is the amount of food in the stomach at the beginning of the experiment (% body dry weight) and the exponent  $R$  is the instantaneous gastric evacuation rate ( $\text{h}^{-1}$ ). In a previous study (Schabetsberger, 1994) this simple exponential function was found to describe gastric evacuation curves in adult and larval alpine newts and it was shown that  $R$  increased exponentially with increasing temperature  $T$  (°C) (coefficients  $\pm$  SE):

$$R = 0.0163(\pm 0.0037)e^{0.07967(\pm 0.0131)T} \quad (2)$$

The time for total emptying of the stomach ( $A_p, \text{h}$ ) can be estimated as the time when 99% of the initial meal is evacuated (Elliott, 1972):

$$A_p = \frac{\ln 100}{R} \quad (3)$$

but due to the asymptotic approach of the evacuation curves to the abscissa small variations in  $R$  will result in large changes in the estimates of gastric evacuation times.  $A_p$  has been found to increase exponentially with increasing body dry weight  $W$  (mg) in preliminary field experiments (Schabetsberger, 1994):

$$A_p = 27.63(\pm 2.35)e^{0.0265(\pm 0.0021)W} \quad (4)$$

Jobling *et al.* (1977), Flowerdew & Grove (1979) and Dos Santos & Jobling (1991) characterized the relationship between  $A_p$  and body weight of fish as:

$$A_p = aW^b \quad (5)$$

with the exponent  $b$  ranging from 0.364-0.389 for fish fed a fixed proportion of their body weight. Consequently  $R$  is expected to decrease with increasing body weight according to either equation (6) or (7):

$$R = ae^{-bW} \quad (6)$$

$$R = aW^{-b} \quad (7)$$

To describe the dependence of gastric evacuation rate on the independent variables temperature and body dry weight ( $R = f(T, W)$ ) the fit of a linear regression plane and two different polynomial surface functions to the data triplets was tested (Dependence of  $R$  on  $T$  and  $W$  either in a double-linear, double-exponential and exponential-root relation):

$$R = a + bT - cW \quad (8)$$

$$R = e^{-a + bT - cW - d} \quad (9)$$

$$R = ae^{bT}W^{-c} - d \quad (10)$$

The numerical values of the constants  $a-d$  are different in equations 5-10. Fitting was performed on a DECstation 5000/33 using the non-linear least squares method implemented in *Mathematica* 2.2. The Marquardt-Levenberg method minimizes the  $\chi^2$  merit function (Press *et al.*, 1992):

$$\chi^2 = \sum_{T=T_{\min}}^{T=T_{\max}} \sum_{W=W_{\min}}^{W=W_{\max}} (R(T, W) - f_R(T, W))^2 \quad (11)$$

where  $T_{\min} = 8^\circ\text{C}$ ,  $T_{\max} = 20^\circ\text{C}$ ,  $W_{\min} = 1.75 \text{ mg}$ ,  $W_{\max} = 39.89 \text{ mg}$ ,  $R(T, W)$  is the gastric evacuation rate measured under the given experimental conditions and  $f_R(T, W)$  is the  $R$ -value calculated with the polynomial in question. The  $\chi^2$  val-

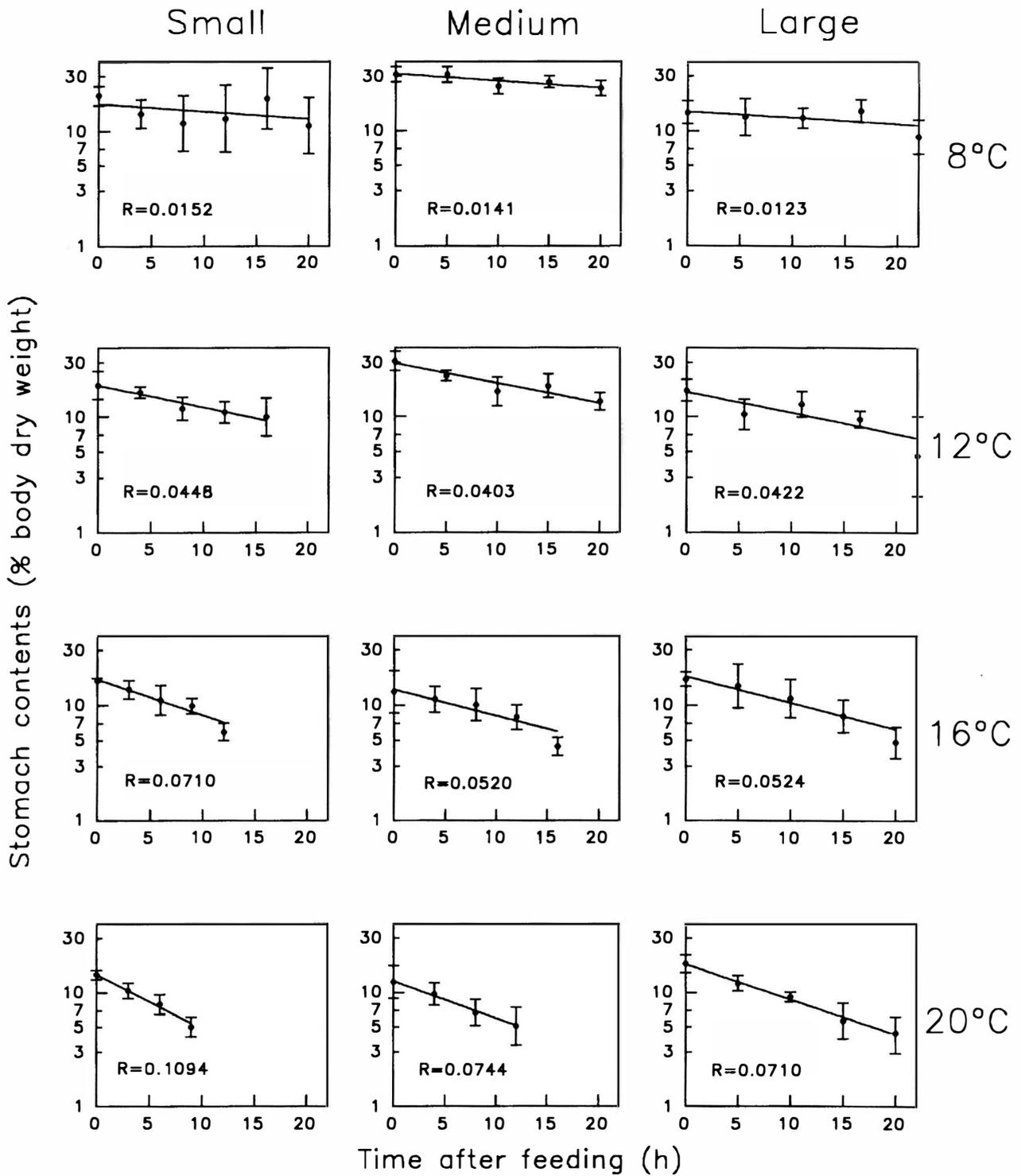


FIG. 2. Semi-log plots of mean stomach contents (% body dry weight) of small, medium and large alpine newt larvae at 4 experimental temperatures in relation to time of starvation (h). Points are geometric means ( $n=30$ )  $\pm$  95% CL. Gastric evacuation rates ( $R, h^{-1}$ ) are shown in each panel.

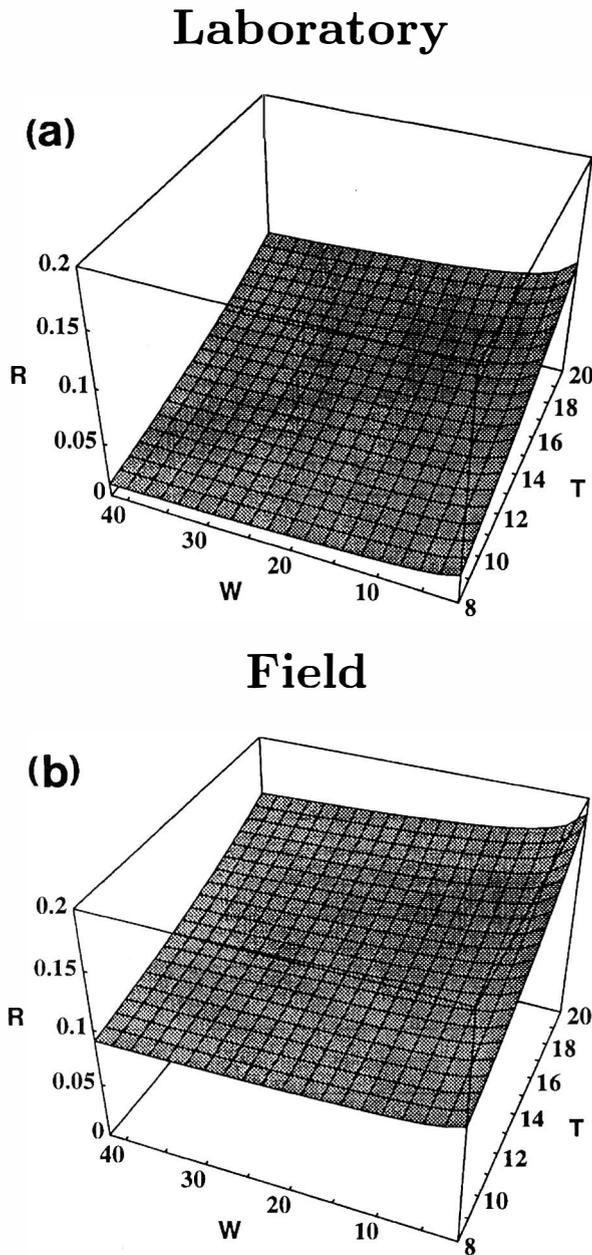


FIG. 3. Three-dimensional grid plots of gastric evacuation rate  $R$  ( $\text{h}^{-1}$ ) in relation to temperature  $T$  ( $^{\circ}\text{C}$ ) and body dry weight  $W$  (mg) of alpine newt larvae. a: laboratory conditions, b: field conditions.

ues were used to compare goodness of fit of the different models.

*Growth of larvae.* Stage of development was determined according to Gallien & Bidaud (1959). They distinguish 56 stages of development between fertilization and metamorphosis. Total length was measured with a vernier calliper. Due to aggressive behaviour of conspecifics, the thin tail tips were frequently damaged under both laboratory and field conditions. Only in the field were we able to collect enough larvae with intact tail tips to perform a geometric mean regression (Ricker, 1975) of dry weight against total length:

$$\log(W) = \log(a) + (b/r)\log(L) \quad (12)$$

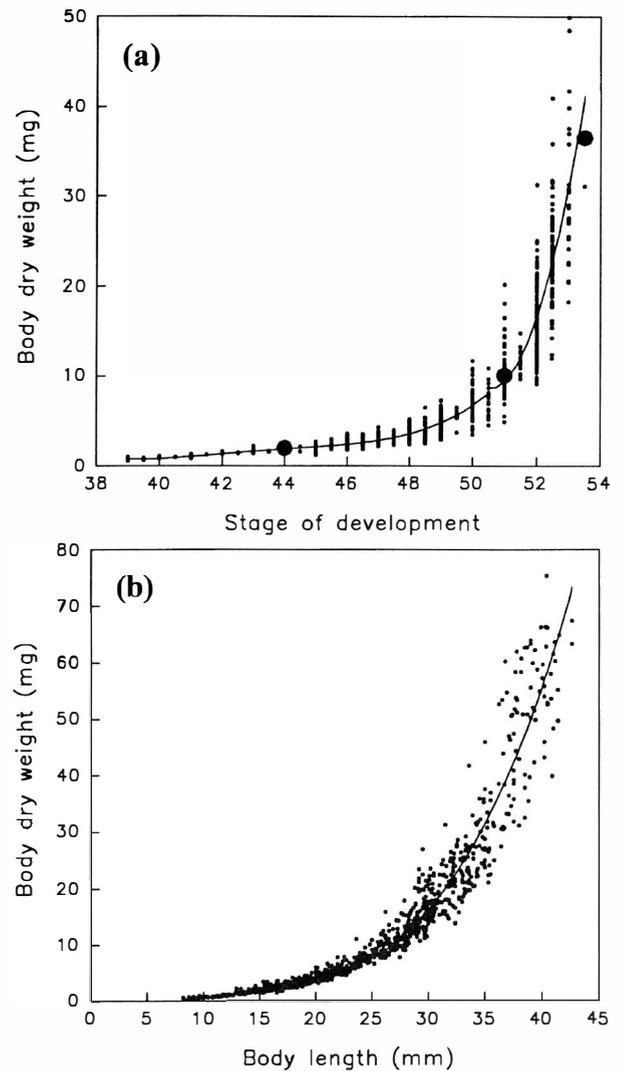


FIG. 4. Growth of larvae. a: Stage of development after Gallien and Bidaud (1959) in relation to body dry weight (mg) of alpine newt larvae collected in the natural habitat ( $n = 948$ ). Mean dry weight of the three size classes of larvae used in the laboratory experiments are shown ( $\bullet$ ). b: Total length (mm) in relation to body dry weight (mg) of alpine newt larvae collected in the natural habitat ( $n = 1066$ ).

where  $W$  = body dry weight without stomach contents (mg),  $a$  and  $b$  are the constants for regression of log weight on log length,  $r$  is the correlation coefficient between log weight and log length, and  $L$  is the total body length of larvae (mm). Only larvae with undamaged gills and limbs were used in the feeding experiments.

## RESULTS

### GASTRIC EVACUATION RATES

For all size classes there was a significant increase in gastric evacuation rate with increasing temperature (small larvae: ANCOVA,  $F=6.82$ ,  $P<0.01$ ; medium sized larvae:  $F=8.26$ ,  $P<0.01$ ; large larvae:  $F=5.28$ ,  $P<0.05$ ; Fig. 2). A significant decrease in gastric evacuation rate with increasing body weight was recorded for the larvae held at  $20^{\circ}\text{C}$  ( $F=12.61$ ,  $P<0.01$ ).

Gastric evacuation rates as a function of temperature and body weight are shown in a grid plot in Fig. 3a. The

relationship was best described by a function of the form given by equation (10) ( $\chi^2=0.00056$ , coefficients  $\pm$  SE):

$$R=0.0301(\pm 0.0049)e^{0.0756(\pm 0.0054)T} \times W^{-0.0846(\pm 0.0061)} - 0.0286(\pm 0.0061) \quad (13)$$

Gastric evacuation rates measured under field conditions were approximately three times faster than those determined in the laboratory (Schabetsberger, 1994), so the function was raised by a constant term to fit the field data ( $\chi^2=0.00673$ , Fig. 3b):

$$R=0.0301(\pm 0.0049)e^{0.0756(\pm 0.0054)T} \times W^{-0.0846(\pm 0.0061)} + 0.0503(\pm 0.0038) \quad (14)$$

A function of the form given by equation (9):

$$R=e^{-2.5698(\pm 0.2225)+0.0433(\pm 0.0058)T-0.0030(\pm 0.0004)W} - 0.0072(\pm 0.0019) \quad (15)$$

gave a similar fit to the field data ( $\chi^2=0.00631$ ) as that of equation (10).

#### GROWTH OF LARVAE

Larvae raised in the laboratory gained weight according to Fig. 4a, describing the relationship between developmental stage and body dry weight of larvae caught in the natural habitat (Schabetsberger & Jersabek, 1995). We fitted fourth and second order polynomials to larvae less and more advanced than stage 51 respectively.

Body dry weight of larvae (mg) caught in the natural habitat could be predicted from total length (mm) using equations (16) and (17) (coefficients  $\pm$  SE). The data were best described by separate equations for larvae of less and greater than 26 mm total length (Fig. 4b):

$$<26 \text{ mm: } W=1.4011 \cdot 10^{-3}(\pm 0.0653) L^{2.6776(\pm 0.0276)} \quad (16)$$

$$>26 \text{ mm: } W=7.6231 \cdot 10^{-6}(\pm 0.0781) L^{4.2844(\pm 0.0657)} \quad (17)$$

#### DISCUSSION

Temperature is a major factor controlling digestion rate in newts. Like fish (Bromley, 1994) gastric evacuation rate increases exponentially with increasing temperature in adult and larval alpine newts (Schabetsberger, 1994; this study). Body weight and the accompanying development of the digestive system had comparatively little effect on rates of gastric clearance in alpine newt larvae. Only during early development did gastric evacuation rates decrease with increasing body weight (Fig. 3), and in larvae  $>10$  mg body dry weight,  $R$ -values were unaffected by body size. Similar results have been obtained in studies on fish larvae and juveniles, with the results being attributed to a growing functionality of the digestive system (Mills *et al.* 1984, Madon & Culver, 1993; Hayward &

Bushmann, 1994). In general  $R$  appears to decrease during development (Doble & Eggers, 1978; Perera & De Silva, 1978; De Silva & Owoyemi, 1983), but in some cases no effect of body weight on digestion rates has been found (Pedersen, 1984; Talbot *et al.*, 1984). Care should be taken not to confuse the exponential rate  $R$ , having the dimension of  $h^{-1}$ , with the absolute rate of gastric evacuation ( $mg \cdot h^{-1}$ ). Although the exponential rate decreases, the absolute amount of food evacuated per unit of time increases during development.

Gastric evacuation rate did not decrease exponentially with increasing body weight as was suspected in a previous study (Schabetsberger, 1994), but a model having the general form of equation (10) also gave a good fit to the field data. A constant had, however, to be introduced in order to account for the faster gastric evacuation of food in the field than in the laboratory (Fig. 3b). The discrepancy between gastric evacuation rates measured under field and laboratory conditions probably resulted from several reasons. In the field experiments the larvae had fed continuously on a variety of prey items such as different species of cladocerans, copepods and chironomids (Schabetsberger & Jersabek, 1995). The meals were comparatively small (3-7 % body weight) and predigested before the start of the experiments (Schabetsberger, 1994). On the other hand the laboratory animals ingested large meals after a period of food deprivation. In two experiments larvae ate more than 30 % of their own body weight (Fig. 2). The long tubificid worms are normally not included in the natural diet. However, we cannot conclude that gastric evacuation rate is generally faster in the wild, because we did not test the laboratory animals at low levels of stomach contents in the range exhibited by wild fish.

These contrary feeding regimes probably resulted in evacuation rates which lie at the upper and lower limits of the physiologically possible. Calculating daily food consumption with the Elliott & Persson model (Elliott & Persson, 1978) using  $R$ -values obtained from equation (13) probably produces minimum estimates, whereas equations (14) and (15) might be used to estimate maximum food consumption in the field. The experiments in the field yielded less precise results than those conducted under controlled laboratory conditions. However, we have still included the weaker field data for basically two reasons. Published estimates of gastric evacuation rates are likely to be used by other researchers to assess the maximum food intake of larvae and their impact on prey populations, as it has been done in many fish studies (Bromley, 1994). Estimating  $R$  from equation (14) at least yields rough estimates of maximum food intake, whereas using equation (13) would probably underestimate food consumption for the reasons mentioned above. Further, equation (14) provides a good fit to all field data ( $\chi^2 = 0.0067$ ), although the underlying  $R$  values were obtained from seven independent experiments with different sized larvae feeding on a variety of food items. We therefore find

that this function describes natural digestion rates sufficiently well.

Although these simplistic equations are strictly speaking only valid under the given experimental conditions, they could be applied to calculate rough estimates of daily rations of other urodele species with similar body size until more information for the species in question is available. A study of digestion in *Notophthalmus viridescens* (Jiang & Claussen, 1993) suggests that evacuation rates are similar within urodeles. However, digestion and evacuation rates of alpine newt larvae appear to be low compared to those of young fish (Govoni *et al.*, 1986) which may consume up to 140% of their own body weight per day (Marmulla & Rösch, 1990; Troschel & Rösch, 1991).

Using equations (16) and (17) it is possible to avoid the tedious determination of dry weight. At hatching larvae grew primarily in length, then later gained considerably more weight per unit length prior to metamorphosis (Fig. 4). This growth pattern may be interpreted as an adaptation to grow out of the food size spectrum of predatory insect larvae (Tejedo, 1993), but more information is necessary before this growth pattern can be explained. Care should be taken when estimating body dry weight from total length using the relationship shown in Fig. 4b, and checks should be made to ensure that the population in question follows the published growth curves. For example, low environmental temperatures retard development and individuals may attain large body size prior to metamorphosis, especially when they overwinter in a pond (Bizer, 1978). If the population in question exhibits different growth rates, *R*-values could be estimated by omitting body weight in equations (13) and (14).

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## HIBERNATION SITES OF THE TOADS *BUFO BUFO* AND *BUFO CALAMITA* IN A RIVER FLOODPLAIN

WILBERT BOSMAN\*, JAN J. VAN GELDER AND HENK STRIJBOSCH

*Department of Ecology, Animal Ecology Section, Catholic University Nijmegen, Toernooiveld 1,  
NL-6525 ED Nijmegen, Netherlands*

*\*Present Address: Stichting ARK, Laag Keppel, Netherlands*

Closed drift fences, bow-nets and a telemetric system were used to study hibernation sites of two toad species in a floodplain. Both species hibernated terrestrially. *Bufo bufo* hibernated in meadows, thickets and woods/bushes on sand or clay in the higher as well as the lower parts of the floodplain. *Bufo calamita* clearly preferred sandy habitats in the higher parts where heaps of brick-debris were specially used. Both species selected their hibernation sites based on characteristics of vegetation and substrate, rather than in relation to the risk of flooding.

### INTRODUCTION

There are only a few anecdotal reports of hibernation of amphibians in floodplains. These concern some adult specimens of frogs (*Rana esculenta* complex, *Rana temporaria*) and larval specimens of newts (*Triturus vulgaris*, *Triturus cristatus*) (in: Creemers, 1991). Hibernation of *Bufo bufo* and *Bufo calamita* has never been studied within a floodplain. Outside floodplains hibernation of both species was studied by Denton & Beebee (1993); that of *Bufo bufo* by Hagström (1982) and van Gelder, Olders, Bosch & Starmans (1986); and that of *Bufo calamita* by Sinsch (1989).

An important feature distinguishing floodplains from other ecosystems is the occurrence of flooding. Amphibians starting hibernation in a dry place, may be flooded during winter. This study reports on the selection of hibernation sites of *Bufo bufo* and *Bufo calamita* in a river floodplain in the Netherlands.

### MATERIALS AND METHODS

#### THE STUDY AREA

All data were collected from 1991 to 1993 in the "Kekerdomse- en Millingerwaard", a floodplain of about 420 ha near the bifurcation point of the rivers Rhine and Waal (6°00' NB, 51°52' WL) in the Netherlands. Almost all floodplains in the Netherlands have been taken into intense agricultural use in the past. The floodplain studied is one of the less cultivated ones, having river dunes, oxbow lakes, small breakthrough lakes and, in the southern and western parts, also fragments of riverine willow woods. The northern and eastern parts are mainly in agricultural use. In one part of this area clay was recently excavated. In the past, two brick factories were situated on higher parts of the floodplain. From one of them the ruins of the old buildings are left. The other one is nowadays used as storage for debris, sand and pebbles.

All floodplains along the river Rhine in the Netherlands are separated from the populated hinterland by a high dyke protecting it against flooding. For agricultural

purposes lower dykes have been built directly on most riverbanks to protect the floodplain itself against flooding during moderately high waters (mainly in summer), thereby decreasing the influence of the river upon floodplains. When the water overflows the lower dyke in our study area 93 % of the floodplain becomes inundated in a very short time. On average this happens once a year (calculated over the period 1901-1980), but it did not happen during our study. Sometimes also the higher, sandy parts of the floodplain become inundated. On average this happens once every ten years. Most floodings occur between December and March, during the hibernation period of most amphibian species (Bosman, 1994). Occasionally the floodplain is flooded during summer.

Seven terrestrial habitat types were distinguished within the area: "woods and bushes" (willow and poplar woods, and willow and alder bushes); "thickets" (high and dense-growing pioneer vegetations of, for example, *Urtica dioica* and *Rubus caesius*); "meadows" (all extensively grazed, lower herb vegetations); "pastures" (intensively grazed grassland); "arable fields" (predominantly maize cultures); "heaps of brick-debris" (the remainders of the brick factory); "sandy areas" (bare sand on river dunes, on the site of the former brick factory and at the bottom of recent clay pits). The waters present in the floodplain were divided into two habitat types: "permanent waters", which contain water throughout the year and "temporary waters", which dry up every year. There are some houses with yards and gardens on the old brick factory site; these were not investigated in this study.

#### DRIFT FENCES

To locate terrestrial hibernation sites we used closed drift fences with pitfalls on the inner side (Gibbons & Semlitsch, 1982; Dodd, 1991). They were made of a plastic film strengthened with an iron mesh and enclosed an area of approximately 32 m<sup>2</sup>. To prevent specimens from climbing in or out of the enclosed area, the top of the foil

was folded 5 cm in and outwards at a height of 50 cm. To prevent specimens from burrowing in or out, the foil was dug 10 cm into the soil. In the enclosed area four pitfalls (10 litre buckets) were placed along the drift fence. The sampled heap of debris was about 40 m in diameter, so the drift fence could not be closed. To catch only amphibians wintering inside this heap, the two ends of the foil were placed as far as possible into the heap's centre. All drift fences were placed in position at the beginning of February and inspected daily after the breeding migration started in early March. From the end of April they were checked once a week only.

The number of drift fences in each habitat type was not proportional to the habitat extent, but depended on the variation within that habitat type, in both the higher and lower parts of the floodplain. For instance the habitat type "woods/bushes" consisted of poplar woods, willow woods, willow bushes or elder bushes whereas "arable fields" consisted of maize cultures only and therefore in the habitat type woods/bushes more drift fences were built (Table 1).

#### BOW-NETS

Our bow-nets consisted of a tetrahedral funnel whose small aperture led into a catching-box. An extension of the catching-box reached the water surface, allowing amphibians to breathe. The larger opening of the funnel measured about 70 cm along the base and it was about 30 cm high. Five temporary waters and five permanent waters were sampled. Each water body got one bow-net. They were installed at the end of December, checked weekly and removed at the start of the breeding migration in spring.

#### MICROTRANSMITTERS

With the aid of microtransmitters (van Nuland & Claus, 1981) implanted in the toads, the exact hibernation sites of six *Bufo bufo* and five *Bufo calamita* were determined. The animals were collected at night in autumn in habitats with an average flooding frequency of once a year (except one *Bufo calamita*, collected at a

higher place in the floodplain). In the laboratory the transmitter was implanted surgically the day after capture. The evening of the same day the tagged animal was released at its site of capture. In the first year of study the presence of the animals in the hibernation sites was checked weekly with a hand-held receiver, in the second year the presence was monitored automatically every hour.

#### RESULTS

With the drift fences 15 *Bufo bufo* were caught. Together with six tagged *Bufo bufo* which hibernated terrestrially this gives 21 specimens hibernating terrestrially. Also all five tagged *Bufo calamita* hibernated terrestrially. Forty-two *Bufo calamita* were caught with the drift fences. So in total 47 *Bufo calamita* were found hibernating terrestrially. No toads were caught with the bow-nets.

Table 2 shows the flooding regimes and the substrate at the hibernation sites of both species. *Bufo bufo* hibernated equally at the higher and the lower parts of the floodplain. All six tagged specimens stayed in the lower parts where they were captured and released. *Bufo calamita* hibernated significantly more often in higher parts, i.e. parts which flood only once every ten years (Fisher's exact test,  $P < 0.001$ ). Three out of four tagged specimens released in the lower parts migrated to the higher parts. The other one remained in the lower part in a sandy place. The fifth specimen, released at the higher part, migrated to the lower part and hibernated in a sandy place too. More, but not significantly more, *Bufo bufo* hibernated at sites with clay. *Bufo calamita* hibernated significantly more often in sandy soils (Fisher's exact test,  $P < 0.001$ ).

Table 3 shows the results of the study with drift fences for each habitat type. Numbers were too low to make a statistical analysis. Comparing both species and taking into account the different number of drift fences per habitat type, it can be inferred that meadows were used equally by both species, woods/bushes were used more by *Bufo bufo*, and sandy areas and heaps of debris

TABLE 1. Number of drift fences placed in each habitat type per flooding frequency. - habitat not present.

Mean flooding frequency:	Every 10 years	Once a year
woods/bushes	3	4
thickets	2	2
meadows	3	3
pastures	-	1
arable fields	-	1
sandy areas	1	1
heaps of brick-debris	1	-
Total	10	12

TABLE 2. Flooding frequency and substrate of the hibernation sites of *Bufo bufo* ( $n=21$ ) and *Bufo calamita* ( $n=47$ ).

	<i>Bufo bufo</i>	<i>Bufo calamita</i>
Flooding frequency:		
every ten years	10	44
once a year	11	3
Substrate:		
sand	7	47
clay	14	0

TABLE 3. Number of *Bufo bufo* and *Bufo calamita* emerged from hibernation per habitat type.

Habitat type	No. of drift fences	<i>B. bufo</i> (n=15)	<i>B. calamita</i> (n=42)
woods/bushes	7	6	0
thickets	4	1	0
meadows	6	7	6
pastures	1	0	0
arable fields	1	0	0
sandy areas	2	0	2
brick-debris	1	1	34

more by *Bufo calamita*. No specimens were found in pastures and arable fields.

All six tagged *Bufo bufo* hibernated in woods/bushes where they were originally captured and released. Three tagged *Bufo calamita* hibernated in a heap of debris after a long migration to this habitat, the other two stayed the winter in meadows.

#### DISCUSSION

In this study we sampled all habitat types in one floodplain using different methods. Houses with yards were not sampled (trespassing was not allowed), but they only covered less than 1% of the floodplain. After the date of placing the drift fences the tagged animals remained at the same locations, so the results of the telemetric research confirm that the timing of placement of the drift fences was well-chosen.

Although toads generally hibernate terrestrially, observations exist (Hagström, 1982) of aquatic hibernation. Indeed, in floodplains, where terrestrial habitats often become flooded during winter, aquatic hibernation could be more common. To check for this the bow-nets were used. In winter-time amphibians are not very mobile. Nevertheless it is possible to catch them with bow-nets then, especially when the water becomes covered with ice during long frost periods. Then oxygen depletion may eventually occur (Bradford, 1983). When bow-nets are checked frequently and thereby are kept free from ice, they form places where the animals can escape from oxygen stress. In another study (unpublished) we caught a number of amphibians under such circumstances. Also in this study we captured small numbers of *Rana temporaria* and *Triturus vulgaris* in the bow-nets placed in temporary waters. As the winter of 1992-1993 was a mild one and therefore the waters were covered with ice only for a short period, some doubt is thrown on the notion of a purely terrestrial mode of hibernation in both *Bufo* species. Nevertheless aquatic hibernation will surely be exceptional. Comparing the results of the drift fences

and bow-nets with those of the telemetric research shows that they are in agreement.

One special purpose of the use of microtransmitters was to study the effect of flooding during terrestrial hibernation. Due to the absence of flooding the effect of this feature remains unknown. Schmid (1965) studied the effect of hydration stress on nine American amphibian species. One, *Bufo americanus*, which is ecologically comparable with *Bufo bufo* and *Bufo calamita*, survived hydration stress for only a few days.

Of all drift fences the highest number of animals was caught in the habitat heaps of brick-debris (Table 3). Besides the species studied, frogs of the *Rana esculenta*-complex and some specimens of *Triturus vulgaris* were also caught there. The heap of debris studied, however, was not enclosed totally (see methods). So the high yield may have been caused by specimens coming from the inner part of the heap and thus enlarging the sampled area. However, in spring 1993 a totally enclosed smaller heap yielded five *Bufo bufo* and 194 *Bufo calamita*. This drift fence enclosed 224 m<sup>2</sup>. Correction for the average surface of the drift fences of this study gives a single *Bufo bufo* and 28 *Bufo calamita*. This result strongly supports the suggested value of our heaps of debris.

As described the heaps of debris are the remnants of human activity in the area. They can be compared with stone heaps on riverbanks, as can be found locally upstream along the river Rhine. As the lower Rhine predominantly transports sand and clay this habitat is absent in the Netherlands.

In our floodplain the most important hibernation sites of *Bufo calamita* (heaps of brick-debris) are situated in a sandy area that seldom becomes flooded. The central part of this area is predominantly bare sand with some young trees of *Populus nigra* and an open pioneer vegetation. At the edges there are some older poplar woods. In a gravel pit Sinsch (1989) found hibernating *Bufo calamita* for the greater part in "Sandy slopes without vegetation". Indeed, the central part of the sandy area, where the heap of brick-debris was situated, seems to correspond with that habitat.

The results of this study show that *Bufo calamita* clearly prefers sandy places for hibernation. In floodplains these places are situated mainly on the higher parts, which seldom become flooded. But they can also be used when present in the lower parts as demonstrated by two of the tagged specimens. These hibernated there in a vegetation of *Calamagrostis epigeios*, which is typical of the higher sand dunes in a floodplain (Bosman, Bekhuis & Helmer, 1993). This suggests that the choice of a hibernation site is determined by the direct suitability of a habitat and not by its flooding frequency. The drift fence study showed that *Bufo bufo* has no preference for the different areas. It appeared to use the same habitat types in the higher and the lower parts of the floodplain (Bosman, 1994). So both *Bufo* species seem to select their hibernation sites

based on the direct suitability of the habitat in the sense of vegetation and substrate, and not by its flooding frequency. Whether specimens that hibernate in the lower parts of the floodplain survive flooding during winter is not known.

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## SEXUAL MATURITY IN A POPULATION OF THE LACERTID LIZARD *PODARCIS BOCAGEI*

PEDRO GALÁN

*Departamento de Biología Animal, Facultad de Biología, Universidad de Santiago de Compostela,  
E-15706 Santiago de Compostela, Spain*

The attainment of sexual maturity by males and females of the lacertid lizard *Podarcis bocagei* was studied in a population from NW Spain (La Coruña province). Two methods were used. The first method involved capture, marking and recapture of marked hatchlings in a study plot. The second method examined the development of sexual organs through dissection of lizard samples from the same locality. Sexual maturity was attained at a minimum size (females: 44-45 mm; males: 46-51 mm snout-vent length), not a minimum age. Some individual and seasonal variation was observed in this minimum size, which decreased as the reproductive season progressed. Slightly fewer than half of the individuals from a given cohort (50.0%-44.4% in males and 47.1%-44.4% in females, from samples of 1989 and 1990 cohorts respectively) attained the minimum size and reproduced towards the end of the next reproductive period (at 11-12 months of age). The mature yearling individuals were those that hatched from the first clutches of the preceding year, most of them in July. By their second autumn, all specimens from the previous year's cohort had exceeded the sexual maturity-threshold size.

### INTRODUCTION

Age and size at sexual maturity are important traits in the life history of an organism. Both can exercise a marked influence on the demographic strategies of squamate reptile populations (Tinkle *et al.*, 1970; Dunham *et al.*, 1988). There are two general strategies of maturation in squamate reptiles: "early" versus "late" maturity. Each of these strategies presumably reflects natural selection favouring successful genotypes under certain environmental conditions (James, 1991). Early maturity may increase life-time reproductive success if there is no reduction in future reproductive output as a result. Late maturity may be more successful if the delay is compensated by larger clutch sizes (as a result of larger body size), or enhanced survival rates (Cole, 1954; Tinkle *et al.*, 1970).

As the rate of growth of reptiles is highly variable, sexual maturity is linked more closely to stage of development or size rather than to age (e.g. Spellerberg, 1982). Among the suborder Lacertilia, sexual maturity is often reached after one or two years, despite considerable variation between species. According to data derived from articles listed in the reviews of Andrews (1982), Dunham *et al.* (1988) and Shine & Schwarzkopf (1992), age at maturity in lizards ranges between 0.65 and 2 yr (data from 28 species or populations), with only two exceptions: *Xantusia vigilis* (3 yr) and *Cyclura carinata* (6.5 yr). In the family Lacertidae, small species also attain sexual maturity between one and two years of age (e.g. Bauwens & Verheyen, 1987; Hraoui-Bloquet, 1987; Barbault & Mou, 1988; Carretero & Llorente, 1991). Nevertheless, larger species attain maturity at an age of 2-4 yr (e.g.

Srijbosch, 1988; Castilla & Bauwens, 1989; Marco & Pérez-Mellado, 1989; Saint Girons *et al.*, 1989).

Reptiles, like most other vertebrates and invertebrates, begin reproducing before they attain their maximum body size. In lizards and snakes, body size at maturation is a relatively constant proportion of maximum size, with a ratio of size at maturity to maximum adult body size generally ranging between 0.50 and 0.90, and an overall mean of 0.71 (Shine & Charnov, 1992). According to Tinkle *et al.* (1970) and Dunham *et al.* (1988), lizards maturing at later age also mature at a larger size, remain larger throughout life, and produce more eggs per clutch than do lizards maturing at an earlier age.

As pointed out by these latter authors, there are two complementary approaches for establishing sexual maturity in reptiles. The first relies upon the recognition of secondary sexual characters or behaviour patterns appearing after sexual maturity. The second relies upon dissection and direct observation of mature gonads or gametes. In this paper, both methods are used to establish size and age of sexual maturity in both sexes of a population of the lacertid lizard *Podarcis bocagei*. The aim was to provide quantitative data on body size and age at sexual maturity in this species, and to describe between-individual and seasonal variation in size and age at maturity.

### MATERIAL AND METHODS

#### NATURAL HISTORY

Bocage's wall lizard, *P. bocagei* (Seoane, 1884), is an endemic species with a restricted distribution in the north-west and west Iberian Peninsula. It is a small,

diurnal, insectivorous lizard of the family Lacertidae. Species of this family are abundant and widespread in the Old World; nevertheless, few accounts of their life histories have been published.

Data obtained during 1989-1991, principally on the basis of mark-recapture experiments but also from laboratory hatching studies (Galán, 1994), show that mating takes place between the end of March and July. The results of this study indicated that during the laying period (from May to July) 8.5% of reproductive females produced three clutches, 52.1% two clutches and 39.4% one clutch. In general, single clutches were produced by small females. Only a small proportion of large females produced three clutches. Mean clutch size was 4.12 eggs (range 2-7). Both clutch size and egg volume increased with maternal SVL. There was no significant between-year variation in clutch size, breeding females' SVL, egg weight or relative clutch mass. Hatching success (as estimated in 1989, 1990 and 1991 from natural nests at the study site) was high, ranging from 83% in 1991 to 91% in 1989.

Dimorphism occurs in this species. The males are bigger than females on average (adult males SVL, 46-65 mm and adult females SVL, 44-63 mm in the population studied) and colour patterns are present during the reproductive period. Adult males show a bright green dorsum whereas females (with few exceptions) have a brown dorsum, like immature lizards (Galán, 1986, 1995; Galán & Fernández-Arias, 1993). The annual activity season of *P. bocagei* from north-western Spain is long. Active individuals can be observed all months of the year; nevertheless, during the winter season (November to January) activity was reduced to basking in the vicinity of winter retreats. The pattern of growth of individuals from the studied population is described by the von Bertalanffy equation (Galán, 1994).

#### STUDY AREA AND AGEING TECHNIQUES

Lizards were studied in a 45 x 60 m plot located in San Vicente de Vigo (45°18' N-8° 20' W; UTM 29T NH5687; 90 m elevation), Carral (province of La Coruña, north-western Spain). The study area was of the wet-oceanic climatic type, characteristic of the coastal areas of the north-western Iberian Peninsula. Average annual rainfall is 1200 mm and average annual sunshine is about 2000 h. Annual temperature oscillation is small, about 10°C between the coldest month (January, mean temperature: 8°C) and the hottest month (July, mean temperature: 18°C). For more details of the study area, see Galán (1994).

Data were gathered during a population study conducted in September 1989-October 1991. Lizards in the study plot were captured by hand, marked individually by toe-clipping, and released after recording identity, sex, reproductive condition, snout-to-vent length (SVL, to nearest 0.1 mm), tail length, and weight (to nearest 0.1 g, on a Pesola® dynamometer).

Age at maturity was investigated by reference to records of juveniles born and marked in 1989 and 1990, and recaptured during 1990 and 1991 respectively. Although a large number of hatchlings were marked (128 in 1989 and 153 in 1990), only 27 (17 females and 10 males) were recaptured between April and July of 1990, and again only 27 (18 females and 9 males) between April and July of 1991. The causes of this low recapture rate (mainly high mortality and dispersal of young age classes) have been discussed elsewhere (Galán, 1994).

Hatching occurred between July and September. Hatchlings have a SVL of 22 to 26 mm (Galán, 1994). Hatchlings of these body sizes collected and marked during July had obviously been born in that month. To determine the time of hatching of hatchlings marked in August and September, the ventral navel scar was examined with a x10 lens. If the navel scar was still open, these individuals had an age of less than 7-10 days (Galán, unpublished data). Average growth rates of hatchlings during their first activity season (from July to September) were 0.186 and 0.142 mm/day, in males and females respectively (Galán, 1994).

Acquisition of sexual maturity by individuals of a population of this species was studied mainly through external signals shown by live animals. Following Tinkle & Ballinger (1972), age at maturity is defined here as age at first breeding rather than age at which mature size is attained. Sexual maturity in the field was assessed in females by noting the presence of enlarged vitellogenic follicles or oviductal eggs, both identified by ventral palpation (pregnant females show a marked distension of the body), or the presence of a mating scar (all mated females that were subsequently recaptured proved to be gravid).

In males it is more difficult to determine minimum age and size at maturity, since they show less evident external signals of sexual activity (e.g. Dunham *et al.*, 1988; James, 1991). Furthermore, both secondary sexual characters and testicular volume decrease towards the end of the breeding season. Sexual maturity was assessed in view of the presence of secondary sexual characters (e.g. bright green dorsum, presence of an enlarged tail base, presence of enlarged femoral pores).

In addition, five males and five females were dissected in each month of the reproductive season to examine their sexual organs and to establish their maturity (total 40 lizards). These lizards were collected from close to the study plot (within 50-500 m of its border), and showed the same size range and external characteristics as those marked in the plot. For each dissected lizard, the following measurements were taken: SVL (to the nearest 0.1 mm); body mass (0.1 g); longest and shortest axes of the right testis; maximum diameter of the right epithelio-epididymis; diameter of the largest ovarian follicle; stage of follicular development (non-vitellogenic, vitellogenic, luteal) and

presence of oviductal eggs. In the text, mean values are cited  $\pm$  standard error of the mean.

## RESULTS

### FEMALES

Body size (SVL) distributions of females of *Podarcis bocagei* collected during each month of the 1991 reproductive season are shown in Fig. 1. Several adult females that still had not begun reproduction in April were considered non-reproductive. Nevertheless, recapture records show that virtually all females that were mature in the previous year showed signs of reproductive activity in May.

The minimal size at which sexual maturity is attained appears to decrease from the beginning to the end of the mating season. In April, the smallest female

found to be gravid by ventral palpation had a SVL of 52 mm; in May, the smallest SVL was 49 mm and in June and July, 44 mm. On the other hand, some females of 50-53 mm SVL did not show signs of sexual activity in May; in June, maximal size of non-reproductive females was 50 mm SVL and in July this maximal size was 45 mm. Thus, the size at sexual maturity in females is 49-53 mm SVL in May, 44-50 mm in June and 44-45 mm in July. The smallest female known to be mature had SVL of 44 mm. Nevertheless, one female, collected about 1.5 km from the study plot, had SVL of 41.7 mm and bore three oviductal eggs; this is the only reproductively mature female of less than 44 mm SVL that I have ever seen (Galán, 1986, and unpublished data).

Body size (SVL) of reproductive females varies significantly between months during the mating season (ANOVA,  $F = 7.41$ ;  $df = 3, 126$ ;  $P < 0.001$ ). A *posteriori* Scheffé test revealed significant differences ( $P < 0.01$ ) between April-July ( $F = 4.45$ ) and between May-July ( $F = 5.24$ ).

Samples of dissected females during each month of the reproductive season show the same minimal body size at maturity as do the records obtained from live specimens (May: 49 mm SVL; June and July: 44 mm).

In females, slightly less than half of the marked individuals of each cohort can reach sexual maturity and reproduce at the age of 11-12 months (Table 1). The 52.9% (1990) or 55.6% (1991) of females remain as subadults until the next breeding season.

Recapture records also show that the individuals that attained the minimum size of sexual maturity before the end of the mating season, and hence participated in reproduction, were born in the first clutch of the previous year (laid in May and hatched in July). In females from the 1989 cohort, individuals that had been born in July had 35.6-40.5 mm SVL (average:  $37.5 \pm 0.66$  mm;  $SD = 1.72$ ;  $n = 7$ ) in autumn 1989, and all lizards of this sample reproduced the following year, in 1990. In contrast, the recaptured individuals of the same cohort that had not attained maturity in 1990 had a smaller body size during au-

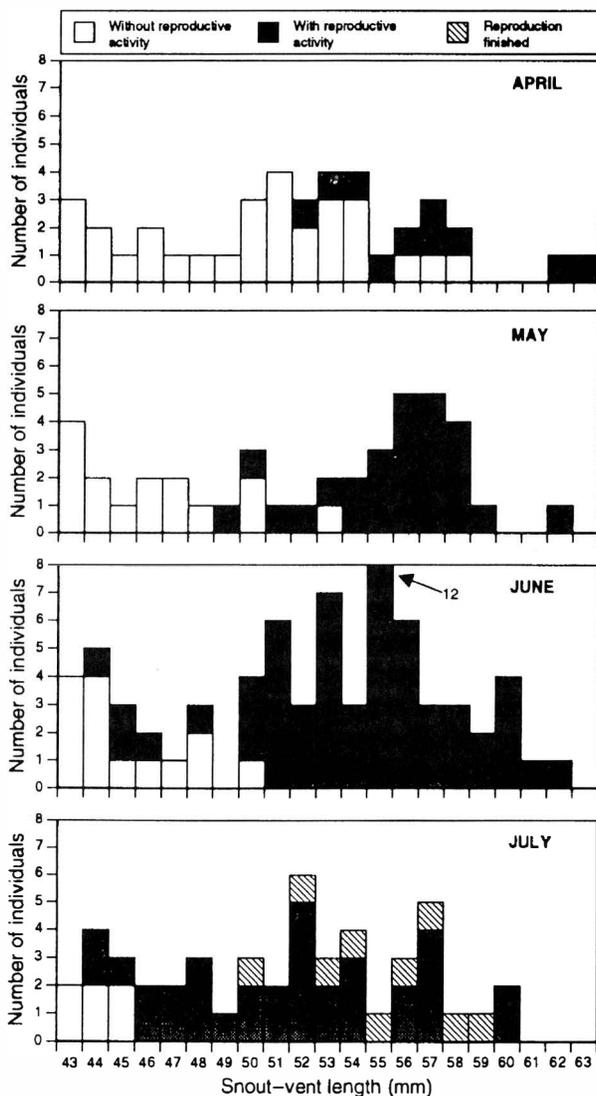


FIG. 1. Body size distribution of female *Podarcis bocagei* collected during each month of the 1991 reproductive season (April to July). These individuals were classified according to whether they showed signs of reproductive activity or not. Signs of reproductive activity were the presence of recent mating scars, or enlarged vitellogenic follicles or oviductal eggs (both noted by ventral palpation).

TABLE 1. Frequencies of lizards of both sexes from the 1989 and 1990 cohorts that attained sexual maturity in each month of the breeding season during their second activity season (one year old). Dates obtained from recapture records in the study plot during 1990 and 1991.

	April	May	June	July	Total	<i>n</i>
1990:					(Jun-Jul)	
Males	0	0	20.0	30.0	50.0	10
Females	0	0	17.7	29.4	47.1	17
1991:						
Males	0	0	11.1	33.3	44.4	9
Females	0	0	16.7	27.8	44.4	18

TABLE 2. Minimal body size and sizes of sex organs of male animals with secondary sexual characters (green dorsal colouration) and clear internal sexual maturity signs (high development and capillarization of testis and epididymis) during every month of the breeding season.

Month	Minimal body size (SVL)	Testicular length	Testicular volume	Epididymis width
April	50.5	4.60	22.84	1.25
May	47.6	3.85	15.52	1.00
June	45.8	4.28	14.00	0.90
July	48.9	3.55	5.69	0.75

tumn 1989: 28.9-35.5 mm SVL (average:  $32.8 \pm 1.22$  mm; SD = 2.98;  $n = 6$ ). These last females came from clutches hatched in the second half of August or September.

#### MALES

Dissection indicated that minimum size at maturity of males (as of females) decreased between April and June of 1990. Nevertheless, in July a strong reduction was observed in both testis and epididymis sizes in all males examined. During this last month, all dissected male lizards smaller than 48 mm SVL were clearly immature (Table 2).

The body size distribution of live males with and without secondary sexual characters collected from the study plot in the 1991 breeding season also show that the minimum body size at maturity of males, like that of females, decreased during the breeding season, from 48 mm (SVL) in May, through 47 mm in June to 46 mm in July. Body size of males that were immature or without reproductive activity likewise decreased from May to June (Fig. 2).

These estimates of minimum size at maturity of males agree closely with estimates based on dissection. The bright green colouration of the dorsal region can thus be considered a reliable external sign of sexual maturity in males of this species, almost throughout the breeding season. On the basis of estimates obtained by both methods, it is considered that the size at which males attain sexual maturity ranges between 46 and 51 mm SVL.

This body size range varies between months. So, in May the variation ranges between 48 mm and 55 mm, in June between 47 and 50 mm, and in July between 46 and 51 mm. In contrast to females, differences were not significant (ANOVA:  $F = 1.26$ ;  $df = 3, 110$ ;  $P = 0.29$ ).

The number of recaptures of yearling males marked as hatchlings was lower than that of females. Nevertheless, a similar pattern in age at maturity was observed in both sexes (Table 1). Approximately half the male cohort attained sexual maturity during its second active season. As for females, recapture records show that yearling males that attain sexual maturity at 11-12 months come from the first clutches of the previ-

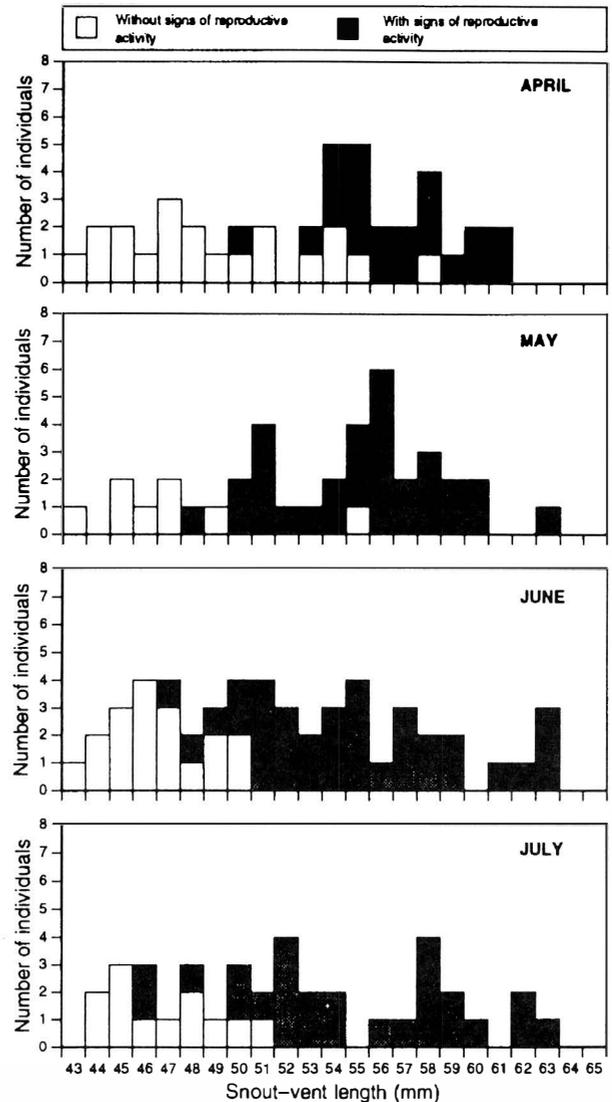


FIG. 2. Body size distribution of male *P. bocagei* collected during each month of the 1991 reproductive season. Signs of reproductive activity were a bright green dorsal colouration and courtship behaviour.

ous breeding season, laid in May and hatched in July. Yearling male lizards, recaptured as mature adults before the end of the 1990 breeding season, had a SVL between 37.3 mm and 40.5 mm (average  $38.7 \pm 0.61$ ; SD = 1.37;  $n = 5$ ) during the previous autumn (October and November 1989). In contrast, males of this cohort that did not attain maturity before the end of the 1990 breeding season had smaller SVL during the preceding autumn (ranged 26.9-37.0 mm; average:  $32.2 \pm 1.73$ ; SD = 3.88;  $n = 5$ ). Recapture records show that these latter males came from clutches hatched in mid-August and September.

#### DISCUSSION

Both sexes of the *Podarcis bocagei* population reached sexual maturity after 11-12 months, at least in the earliest hatchlings (early July until mid-August). This age is attained in mid-June or July. They then begin reproduction immediately (in the case of females, see below). For hatchlings born in mid-August to mid-

September, sexually mature size would be reached in late summer or autumn of their second activity season, an inappropriate time for reproduction. Their first breeding would be in the subsequent spring (third activity season). So these belong in the class categorized as "delayed maturing" (Tinkle, 1969). This pattern has been described in several lizard species (e.g. Tinkle & Ballinger, 1972; Dunham *et al.*, 1988) and is a frequent event in small Mediterranean lacertids (e.g., Henle, 1988; Carretero, 1993). In contrast, in bigger lacertid species, sexual maturity is always later, with differences between the sexes (e.g. Castilla, 1989; Marco & Pérez-Mellado, 1990; Marco, 1994).

Sexual maturity in *Podarcis bocagei* is related to the attainment of a minimal body size and not a minimal age, as in other lacertids (Heulin, 1985; Bauwens & Verheyen, 1987). Differences in age at maturity between individuals of the same cohort may be a direct consequence of the long hatching season (July to September). On the other hand, particular events (such as diseases or injury) delay growth (Galán, 1994) and may also cause differences in age at maturity.

High variability (both among individuals and within-season) was also observed in the minimal body size at which sexual maturity is attained by females. Over the reproductive season, minimum size at maturity decreases significantly. The widest among-individual range was that observed in July 1990 (41-45 mm), although 41 mm appears to be exceptionally small. In many other populations of *Podarcis bocagei* from north-western Spain, adult females smaller than 44 mm SVL have not been recorded (Galán, 1986 and unpublished data). Many other authors have described a high variability in the size and age at sexual maturity in female lizards, but this variability is between different populations of the same species (e.g., Bauwens *et al.*, 1986) or between different years within the same population (e.g., Bauwens & Verheyen, 1987). In the study population, variability occurs within the same population and year.

Individual differences in minimal body size at maturity within the same period can be related to differences in the amount of lipid stores between young females. These fat bodies are necessary for vitellogenesis and egg development (e.g. Braña *et al.*, 1992 for northern Spain *P. bocagei* populations). Thus, female lizards that have not obtained enough lipid for egg production at the end of the reproductive season (in July), cannot reproduce even though they have attained the minimal body size for maturity.

It is important to point out that the young females that mature sufficiently early in the breeding season to produce one clutch grow more slowly during the second half of the summer than the other females of the same age that did not reproduce. This may be due to the high energy expenditure involved in the egg production for yearling females. At the end of the activity season, the body size of yearling mature females may be smaller than that of females that did not reproduce.

For example, of two yearling female lizards of approximately the same body size during July, the female that did not reproduce (45.6 mm in July) attained 53.8 mm SVL in the following autumn (November), whereas the female that laid three eggs (45.8 mm) attained 51.5 mm SVL in the same time.

During autumn, female *P. bocagei* classified as adults on the basis of size are, in fact, two classes: adult females that produced eggs and adult females that did not. The same pattern was observed by Andrews (1989) in a population of the tropical lizard *Anolis limifrons* and he gave this observation particular importance. In studies of lizard population dynamics, a large proportion of immature females can be considered to be mature and producing eggs if the sole criterion is body size during pre- and postreproductive seasons. In this population, during the autumn and following spring, several females that had not laid eggs in the previous breeding season had a larger body size than females of the same cohort that had reproduced and laid eggs in that period. In females that had not reproduced, energy was allocated only in growth and in this way they attained a larger body size than females that diverted a proportion of their energy to egg production (see also Andrews, 1979, 1989).

One clear result, despite often wide variation in size at maturity, is that males matured at a larger SVL than females: 46-51 mm versus 44-45 mm. Nevertheless, both sexes matured at the same age, between one and two years and also with a similar proportion between these two ages in each sex: slightly fewer than half of each cohort. As in the case of females, differences in age at maturity can be related to the hatching period and, consequently, to the amount of time for growth between different individuals.

It is interesting to point out that the attainment of sexual maturity in yearling males does not necessarily imply that they participate in reproduction that year, as in the case of adult yearling females. In young females, all individuals that attain sexual maturity before the end of the mating season are mated and produce eggs (Galán, 1994). Direct field observation shows that smaller adult males with recent attainment of sexual maturity (clear presence of secondary sexual characters, but small size), are unable to win in contests with larger males. In all encounters between a yearling adult male and a two or more year-old male observed in the field ( $n = 17$ ), young males showed submissive behaviour (tail lashing and "Treteln" displays) and flight. So, recently matured males can have access to females and mate only in the absence of the full adult males. Consequently most of them probably do not mate until their third activity season.

Shine & Charnov (1992) observed that, in lizards and snakes, body size at maturity is a relatively constant proportion of maximum size. The mean ratio of size at maturity to maximum body size in the lizard species studied by these authors was 0.74. In the population of *P. bocagei* studied here, maximum adult body

size (SVL) is 65 mm in males and 63 mm in females. Thus, the ratios obtained were 0.71-0.78 in males, and 0.70-0.71 in females. All of these values are very close to the overall mean given by Shine & Charnov (1992).

Maintenance of a high variability in age and, to a certain extent, body size at maturity, presumably reflects an adaptation to unpredictable environments, as observed in the studied *Podarcis bocagei* population. This lizard population lives in a place with pronounced slopes and uncovered excavated land (a gravel pit and surrounding areas) which was rapidly recolonized by opportunistic vegetation (Galán, 1994). Excavation for gravel creates new derelict uncovered areas, which again suffer the process of plant recolonization. In these environments, as in others such as urban areas, the edges of cultivated areas, trenches, etc. (all of them typical small lacertid lizard habitats, see Arnold, 1987) may favour the maintenance of high variability in the life-history strategies for facing different selection pressures.

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## SHORT NOTES

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**PREGNANCY DECREASES SET  
POINT TEMPERATURES FOR  
BEHAVIOURAL  
THERMOREGULATION IN THE  
WALL LIZARD *PODARCIS MURALIS***

GIANLUCA TOSINI\* AND ROGER AVERY

*School of Biological Sciences, University of Bristol,  
Bristol BS8 1UG, UK*

*\*Present address: Department of Biology, Gilmer Hall,  
University of Virginia, Charlottesville, VA 22903, USA*

Pregnancy in females is one of the many factors which can affect the activity temperatures of lizards (Huey, 1982). Body temperatures or selected temperatures increase during pregnancy in four species (*Hoplodactylus maculatus*, Werner & Whitaker, 1978; *Gerrhonotus coeruleus*, Steward, 1984; *Chalcides bedriagai*, Hailey, Rose & Pulford, 1987; *C. ocellatus*, Daut & Andrews, 1993). They fall in five others (*Sceloporus cyanogenys*, Garrick, 1974; *S. jarrovi*, Beuchat, 1986; *S. virgatus*, Andrews & Rose, 1994; *Lacerta vivipara*, Van Damme, Bauwens & Verheyen, 1986 and Heulin, 1987; *Podarcis muralis*, Braña, 1993).

Because body temperatures appear to respond to pregnancy in different lizard species in different ways, therefore, we were prompted to make a careful laboratory study of the effects of pregnancy on set point temperatures (defined in Tosini & Avery, 1993) in the European wall lizard, *Podarcis muralis*, as part of a long-term study of behavioural thermoregulation in this species using infra-red thermography. The results are presented here.

*Podarcis muralis* are small lizards (adult body mass is usually within the range 5-10 g) which are distributed over a wide area in central and southern Europe. The specimens used here were ten female lizards collected in the vicinity of Florence (Italy) in May 1991. They were transferred to the laboratory, and maintained under an illumination cycle of 8 h light: 16 h dark. Heat for thermoregulation during the light phase was provided by tungsten reflector bulbs. All of these lizards turned out to be pregnant. Their thermoregulation was studied during the period when they were heavily distended with eggs in the second half of June, and again in late July after they had laid their eggs. Comparisons were made with (a) data for other female lizards which had been captured near Florence in 1990, maintained under the conditions described above, and studied during the early spring of 1991 (these lizards had not had access to males, and were not pregnant; the three categories of female lizards de-

scribed above are referred to as 'during', 'after' and 'before' pregnancy, respectively) and (b) male lizards maintained under similar conditions and also studied during early spring of 1991.

Individual lizards were transferred singly to experimental arenas, where they were able to thermoregulate for 8 h per day, beginning at 10:00 h, using radiant heat from a 60 W tungsten reflector bulb set at such a height that it provided an irradiance of 58 mW cm<sup>-2</sup> at the point immediately beneath it. Under these conditions the lizards usually alternated periods of basking beneath the bulb with periods of movement around the arena (foraging). Values for four thermoregulatory variables ( $T_{\text{bask}}$ ,  $T_{\text{move}}$ , mean bask duration and mean duration of the periods of foraging between basks) were determined using an infra-red vidicon camera; the use of this equipment to determine set point temperatures is described in detail in Tosini & Avery, 1993:  $T_{\text{bask}}$  is the lower set point temperature, measured at the point when a lizard begins basking;  $T_{\text{move}}$  is the upper set point temperature, measured when it ceases basking (definitions in Jones & Avery, 1989). Total sample sizes for each variable were before pregnancy  $n = 80$  (eight lizards), during pregnancy  $n = 100$  (10 lizards), after pregnancy  $n = 110$  (the same 10 lizards). Since set point temperatures change on a diel cycle (Tosini & Avery, 1994), all measurements were made between 11:00 - 13:00 GMT. The frequency distributions of set point temperatures showed significant skewness and kurtosis, and so statistical analyses are in terms of both mean (parametric tests) and median (non-parametric tests) values.

Table 1 shows the mean overall values for the four thermoregulatory variables before, during and after pregnancy. Experimentally-determined values for the four variables considered ( $T_{\text{bask}}$ ,  $T_{\text{move}}$ , bask duration and forage duration) did not differ among animals in the same group (Friedman tests,  $P > 0.1$  in all cases). Both mean set point temperatures were significantly lower in all the pregnant lizards tested with respect to the values recorded before and after pregnancy (Multiple Comparison tests (Siegal & Castellan, 1988),  $P < 0.05$ ). Variances of  $T_{\text{move}}$  were in all cases lower than variances of  $T_{\text{bask}}$  ( $F = 1.66-1.99$ ,  $P < 0.05$ ). In all the individuals tested, mean bask duration in pregnant lizards was longer (Multiple Comparison tests,  $P < 0.05$ ). The separation of set point temperatures (i.e.  $T_{\text{move}} - T_{\text{bask}}$ ) was smaller in pregnant lizards (Multiple Comparison tests,  $P < 0.05$ ). Mean durations of forages between basks did not differ among the three conditions (Friedman test,  $P > 0.1$ ).

The reductions in set point temperatures, and hence the mean activity temperatures, recorded here are consistent with previous studies of Lacertidae (Van Damme *et al.*, 1986; Heulin, 1987; Braña, 1993). The first two of these studies relate to *Lacerta vivipara*. The third relates to *P. muralis*, and demonstrated that pregnant females had lower body temperatures in the field, but not when measured in a thermal gradient (Braña,

TABLE 1. Mean and median values for the variables  $T_{\text{bask}}$  and  $T_{\text{forage}}$  ( $^{\circ}\text{C}$ ), and mean values for bask duration and forage duration (min) before, during and after pregnancy.

	<i>Before</i>			<i>During</i>			<i>After</i>		
	mean	SD	median	mean	SD	median	mean	SD	median
$T_{\text{bask}}$	34.0	0.84	34.1	32.1	1.28	32.1	34.0	0.86	34.0
$T_{\text{move}}$	38.8	0.60	38.9	36.2	0.99	36.2	38.8	0.66	39.0
Bask duration	1.5	0.64	-	2.3	1.41	-	1.7	0.87	-
Forage duration	3.2	2.30	-	4.0	2.72	-	3.9	2.81	-

1993). It was suggested that the changes in recorded body temperatures were not a consequence of changes in thermal preferences, but a result of constraints imposed passively by changes in overall behaviour (see also Bauwens & Thoen, 1981). The changes in set point temperatures recorded here demonstrate that this is not the case; central thermoregulatory mechanisms (Firth & Turner, 1982) must be involved.

The set point temperatures of pregnant lizards are likely to have evolved as a result of compromises between potentially conflicting pressures such as physiological optima for embryonic development, physiological optima for the female, and ecological constraints (Beuchat, 1986, 1988; Beuchat & Ellner, 1987; Daut & Andrews, 1993). The optimum temperature for embryogenesis in *P. muralis* lies within the range 24–32 $^{\circ}\text{C}$ , and is probably close to 28 $^{\circ}\text{C}$  (Van Damme, Bauwens, Braña & Verheyen, 1992). Since this lies below the normal activity temperature range of the species (Avery, 1978; Braña, 1990; Van Damme *et al.*, 1992), the shift is probably adaptive.

There is an alternative - and not mutually exclusive - explanation. Total body mass may increase by more than 30% in pregnant *P. muralis* (unpublished data). The ability to flatten the body while basking, which in non-pregnant females can increase the dorsal surface area between the pectoral and pelvic girdles by up to 40% (unpublished data), is impaired. Heating rates during basking are therefore reduced; since the value for ( $T_{\text{move}} - T_{\text{bask}}$ ) changes only slightly, the time spent basking increases (Table 1). This may increase the vulnerability of pregnant animals to predation (Bauwens & Thoen, 1981; Braña, 1993). There will thus be a selective advantage in reducing mean body temperatures, since overall basking times will then fall.

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**ADVERTISEMENT CALLS OF THREE  
GLASS FROGS FROM THE ANDEAN  
FORESTS (AMPHIBIA: ANURA:  
CENTROLENIDAE)**

RAFAEL MÁRQUEZ<sup>1</sup>, IGNACIO DE LA RIVA<sup>2</sup>,  
AND JAIME BOSCH<sup>1</sup>

<sup>1</sup>*Dept. de Ecología Evolutiva; Museo Nacional de  
Ciencias Naturales; C/ José Gutiérrez Abascal 2. 28006  
Madrid, Spain*

<sup>2</sup>*Natural History Museum, The University of Kansas,  
Lawrence, Kansas 66045-2454, USA*

<sup>2</sup>*Permanent Address: Departamento de  
Biodiversidad y Biología Evolutiva, Museo Nacional de  
Ciencias Naturales. C/ José Gutiérrez Abascal 2, 28006  
Madrid, Spain*

Centrolenid frogs form a family of anurans that is distributed from Mexico to Argentina, with the highest diversity of species in the Andes of Colombia and Ecuador. New species have been described at a high rate in the last years: 56 species were reported by Duellman (1977), 60 by Frost (1985), 94 by Duellman (1993), and 104 by Wild (1994). Most recent papers on centrolenid frogs deal with alpha-level taxonomy. A noteworthy contribution to the knowledge of the systematics of the family has recently been completed by Ruiz-Carranza & Lynch (1991), whereas Sanchiz & De la Riva (1993) pointed out the need for a reassessment of the consistency of a character that has been always considered as the most important synapomorphy of the family, namely, fusion of tibiale and fibulare.

Information on the natural history, ecology, and other aspects of most species of centrolenids is extremely scarce. The area of bioacoustics is one such poorly studied area. Unlike other Neotropical groups of anurans for which more comprehensive information on vocalizations is available, next to nothing is known on centrolenids. In general, their calls are high frequency notes. This has been related to the small size of these frogs and also to the fact that this kind of sound is suitable for propagation in the environment where these frogs primarily occur, namely, streams surrounded by dense plant cover (Richards & Wiley, 1980; Wells & Schwartz, 1982).

Syntopically occurring species of glass frogs may have generally similar external appearances and often they have to be identified on the basis of a combination of characters. The great species-specificity of the vocalizations in anurans (for a review of this subject, see Duellman & Trueb, 1986), makes the descriptions of the advertisement calls, useful tools for recognising different species. Accurate descriptions of the adver-

tisement calls of centrolenid frogs are only available for a handful of species (Barrio 1968; Starrett & Savage, 1973; Heyer, 1978, 1985; Greer & Wells, 1980; Haddad, Andrade & Cardoso, 1988; Cadle & McDiarmid, 1990; Heyer, *et al.*, 1990; Ibáñez, 1993; Señaris & Ayarzagüena, 1993). In this study we contribute to the knowledge of the centrolenids of Bolivia and Ecuador by describing the previously unknown advertisement calls of three species, in addition to providing notes on their calling behaviour and distribution.

Recordings were obtained by the second author from 1987 to 1990. Recording equipment included either a Sony WM D6C or a Sanyo M1120 tape recorder and a Sennheiser Me 80 directional microphone. We present a representative audiospectrogram and oscillogram for a selected 2.5 sec recording segment for each species. A longer recording (20-60 secs.) was analysed when available to generate numerical information on the spectral and temporal characteristics of the sounds. Recordings were processed with a digital signal analysis system based on an Apple Macintosh. The sounds were digitized and edited at a sampling frequency of 44.1 KHz and 16 bit resolution with 'Sound Tools' hardware and software. Signalyze software was used to obtain numerical information and to generate audiospectrograms and oscillograms. Frequency information was obtained through fast Fourier transform (FFT) (width, 1024 points). The terminology used for the description of the advertisement calls follows Heyer *et al.* (1990). Unless specified, classification and nomenclature of the species follow Frost (1985).

Seven different call characteristics were recorded. The variables considered were: note duration, fundamental frequency, dominant frequency, other frequency with substantial energy, number of pulses per note, pulse rate (pulses per second), and change in dominant frequency (dominant frequency at the end of the note minus dominant frequency at the beginning of the note). Collected individuals of *Cochranella bejaranoi* and of *Hyalinobatrachium bergeri* were deposited in the Centro de Estudios Tropicales, Sevilla, Spain, and/or in the Museo de Historia Natural "Noel Kempff Mercado", Santa Cruz de la Sierra, Bolivia. No specimens were collected in Ecuador.

*Centrolene ballux* (Duellman & Burrowes, 1989) occurs in cloud forests on the Pacific versant of the Andes, Departamento de Nariño, Colombia, to the Provincia de Pichincha, Ecuador (Duellman & Burrowes, 1989). The advertisement call of *C. ballux* was recorded in Las Palmeras, ca. 1400 m, Pichincha, Ecuador (00° 17' S / 78° 45' W). The air temperature during the recording session was approximately 20°C. Males called at night, perched on large leaves of riparian trees at about 2 m. above ground. The call was emitted sporadically. The call was a single, relatively short note ( $n=2$ , mean duration 374.5 ms, SD 70, range 328.5-420.4) with 7-9 pulses (not 100% amplitude

modulated), the first 4-5 being repeated at short, regular intervals, and the last three pulses being emitted at longer intervals (mean pulses per second 21.4, SD 0.1, range 21.3-21.4) (Fig. 1A). The dominant frequency was high (mean dominant frequency at peak amplitude 4833 Hz, SD 209, range 4685-4981) and the call had an upwards frequency sweep (mean increase + 454 Hz, SD 14, range 444-464). The animals recorded were calling in the near vicinity of a fast flowing stream that produced a loud white noise below 4000 Hz. The frequency band occupied by the call was right above the noise band of the stream (filtered out in Fig. 1). *Hyla carnifex* called simultaneously at the same place.

*Cochranella bejaranoi* (Cannatella, 1980) is a Bolivian endemic occurring in cloud forests of the Amazonian Andean slopes. Previously known only from the type locality (51.8 km SW Villa Tunari; Cannatella, 1980) and a nearby locality (De la Riva, 1990), it has now also been found at Sehuencas, 2300 m, Departamento de Cochabamba (17° 29' S / 64° 16' W), several localities in the La Siberia region (boundary between the departments of Cochabamba and Santa Cruz), and La Yunga, 2000 m, Departamento de Santa

Cruz (18° 06' S / 63° 54' W). Advertisement calls of male *C. bejaranoi* were recorded in La Siberia, Río Chua Kocha, Provincia de Carrasco, Departamento de Cochabamba, 2000 m (17° 47' S / 64° 42' W). Air temperature at the time of recording was 14°C. Males called while perched on stems of understory vegetation (such as ferns), near streams, at approximately 1.5 m. above the ground. Isolated males called at night, the calls being repeated at long (up to several minutes), irregular intervals. The call (Fig. 1B) was a sequence of 6-7 pulses the first six being repeated at regular intervals (mean interval 9 ms), and the last one being more separated (mean interval 42 ms) (mean pulses per second 33.3). Mean call duration was 202.3 ms ( $n=4$ , SD 9.3, range 189.1-210.6). The mean dominant frequency was of 4039 Hz (SD 103, range 3887-4113), and the call increased slightly in dominant frequency (mean increase + 168 Hz, SD 23, range 373-505).

*Hyalinobatrachium bergeri* (Cannatella, 1980) occurs in forests on the Andean Amazonian slopes, from the Departamento de Cuzco, Perú, to the Departamento de Santa Cruz, Bolivia. Although initially reported exclusively as a cloud forest-inhabiting species ranging from 1700-1890 m (Cannatella, 1980), we found it in Bolivia at the foot of the mountains, at localities as low as 300 m. a. s. l., such as in Paractito, department of Cochabamba (17° 01' S / 65° 27' W), and in Amboró National Park, department of Santa Cruz. Additionally, Emmons (1991) reported the species at 13 km W Ixiamas, Department of La Paz. Recordings were obtained at Río Cheyo, 700 m, Amboró National Park, Province Ichilo, Department of Santa Cruz, Bolivia (18° 40' S / 63° 35' W). Males called at night from the underside of the leaves of riparian trees at about 2.5 m above ground. Air temperature at the time of recording was 19°C. The call (Fig. 1C) was a short note ( $n=15$ , mean duration 151.4 ms, SD 21.6, range 125.5-169.4), with a mean dominant frequency at peak amplitude of 4495 Hz (SD 74, range 4402-4558), and a marked upwards (logarithmic) frequency sweep (mean increase + 449 Hz, SD 61, range 373-505). A well-tuned second harmonic showed substantial power of 9149 Hz (SD 158, range 8925-9268). No other anuran species could be heard concomitantly.

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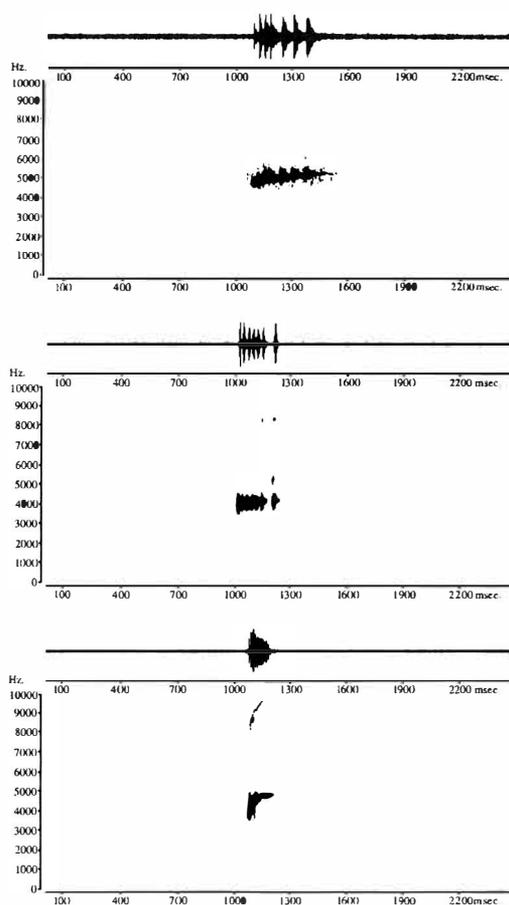


FIG. 1. Audiospectrograms and ocollograms of a 2.5 s section of a characteristic advertisement call. A, *Centrolene ballux*; B, *Cochranella bejaranoi*; C, *Hyalinobatrachium bergeri*. Note that the ordinate for the ocollogram is relative and linear, and therefore a scale is not provided.

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## HOME RANGE AREA OF THE LIZARD *PODARCIS HISPANICA* *ATRATA*

JOHN G. SWALLOW<sup>1</sup>\* AND AURORA M.  
CASTILLA<sup>2,3</sup>

<sup>1</sup> Department of Zoology, Birge Hall, 430 Lincoln Drive,  
University of Wisconsin, Madison WI 53706, USA

<sup>2</sup> Department of Biology, University of Antwerp (UIA),  
B-2610 Wilrijk, Belgium, and <sup>3</sup> Institut d'Estudis  
Avançats de les Illes Balears (CSIC), Ctra.  
Valldemossa, Km 7,500, E-07071 Palma de Mallorca,  
Spain

Home range is defined as the area traversed during the routine activities of food gathering, mating, seeking shelter, and caring for young (Burt, 1943). Studies of home range area (HRA) have been of enduring interest to population and behavioral ecologists (Turner, Jennrich & Weintraub, 1969; Christian & Waldschmidt, 1984; Garland, Dickerman, Janis & Jones, 1993). The aim of this study was to measure the home range area of the lizard *Podarcis hispanica atrata*. *Podarcis h. atrata* is an endangered heliothermic lizard endemic to the Columbretes islands (Castilla & Bauwens, 1991a,b; Castilla & Swallow, 1995). This is an actively foraging species that feeds mainly on arthropods (Castilla, Jiménez & Lacomba, 1987), although it also preys on conspecific eggs and juveniles (Castilla, 1995).

The Columbretes islands (39° 54' N, 0° 41' E) constitute an archipelago of small uninhabited islands of volcanic origin situated in the Mediterranean ca. 57 km off the coast of Castellón (province of Castellón, Spain). The climate of the archipelago is characterized by an average annual temperature of 17°C and low rainfall (265 mm/year). This lizard is present only on four islets, having an entire range of about 20 ha.

The study was conducted on the largest (13 ha) island, 'Columbrete Grande,' where the density of lizards in favourable habitats is very high (> 800 individuals/ha; Castilla & Bauwens, 1991b). The study site was a grid (2,800 m<sup>2</sup>) marked with coloured flags on 1.5 m metallic wires spaced 5 m apart; each flag was marked with an ordinal coordinate. Vegetation in the study site consists mainly of perennial shrubs (*Suaeda vera*, *Lobularia maritima*) not higher than 60 cm, herbs (*Lavatera mauritanica*), and patches of grasses. The study plot was visited every day during 27 May - 1 July 1993 (34 days) between 0800-1100 and 1500-1900 hrs (Mean European Time, MET). A total of 96 adult lizards was captured by noose or by hand. We considered lizards with snout-vent length (SVL) > 50 mm as adults. Males were distinguished from females by head shape, and presence of femoral pores (Castilla & Bauwens, 1991b). Data recorded for each lizard in-

cluded date of capture, site of capture (by cardinal ordinate), sex, SVL, and body mass. SVL was measured to the nearest 0.1 mm with callipers, and mass was measured to the nearest 0.1 g with a pesola scale. An individual identification code (four colour dots marked with paint spots on the back of the head and neck) was given to each lizard. The lizards were then released at their point of capture. Subsequent sightings and recaptures were recorded only with date and site of capture. Recapture data for an individual lizard caught within four hours of a previous recapture were discarded to minimize autocorrelation between data points and to allow lizards to return to their normal activity.

HRA was estimated using the convex polygon method (Waldschmidt, 1979; Rose, 1982) because this estimate can easily be graphed and visualized with a co-ordinate system. Furthermore, with adequate numbers of recaptures, estimation by convex polygon provides an accurate and comparable measure of HRA (Rose, 1982). Multiple regression analyses were used to estimate log HRA with log body mass, number of captures, interval between first and last capture, and a dummy variable for sex as independent variables. All analyses were performed using SPSS/PC+ version 5.0.

SVL ( $\pm 1$  SE) averaged  $62.4 \pm 4.89$  mm (range 53.0 - 74.1 mm;  $n = 61$ ) for adult males, and  $59.2 \pm 3.54$  mm (range 52.0 - 65.2 mm;  $n = 35$ ) for adult females. Body mass averaged  $5.4 \text{ g} \pm 1.25 \text{ g}$  (range 3.6 - 8.5 g;  $n = 61$ ) for adult males and  $4.0 \text{ g} \pm 0.68 \text{ g}$  (range 2.8 - 5.5 g;  $n = 35$ ) for adult females. Adult males were longer (ANOVA:  $F_{1,94} = 11.28$ ;  $P < 0.001$ ) and heavier (ANOVA:  $F_{1,94} = 41.01$ ;  $P < 0.001$ ) than females. ANCOVA indicated that males weighed more than females even after accounting for differences in SVL ( $P < 0.001$ ). Allometric equations were:  $\log \text{body mass} = -4.14 + 2.71 \times \log \text{SVL}$  ( $R^2 = 0.823$ ; 95% CI on slope = 2.384 - 3.038) for males, and  $\log \text{body mass} = -3.81 + 2.48 \times \log \text{SVL}$  ( $R^2 = 0.749$ ; 95% CI on slope = 1.975 - 2.993) for females.

HRA was calculated for all individuals which were captured five or more times (mean = 12.5; Table 1). However, inspection of the relationship between cumulative HRA and number of recaptures indicated that many of the lizards may not have been recaptured a sufficient number of times to accurately predict HRA. As noted by many authors, an insufficient number of recaptures results in an underestimation of HRA (Jennrich & Turner, 1969; Schoener, 1981) whereas the use of a correction factor often leads to an overestimation of HRA (Rose, 1982).

A multiple regression approach was used to estimate HRA, accounting for log body mass, number of recaptures, interval between first and last recapture, and sex. We used a stepwise algorithm and various combinations of forced entry to determine the best model. Based on previous studies, we expected HRA to increase with increasing body mass, number of recaptures, and interval between first and last capture. We also anticipated that males would maintain a larger

TABLE 1. Home range size (HRA), number of captures, interval between first and last capture, sex, body mass, and snout-vent length (SVL) for individual adult male (M) and female (F) lizards with at least five captures.

HRA (m <sup>2</sup> )	No. captures	Interval (days)	Sex	Mass (g)	SVL (mm)
123.5	27	27	M	6.1	66.1
50	23	34	M	5.8	63.6
75.5	21	26	M	5.0	59.1
54	21	21	M	5.3	62.0
165	20	29	M	6.7	65.7
109	20	27	M	8.1	74.0
34	20	21	M	4.2	57.6
61	15	16	M	7.4	67.3
34.5	15	18	M	5.6	60.8
39	14	17	M	6.2	65.9
111.5	12	29	M	6.8	67.2
67	10	14	M	8.5	72.1
26.5	8	12	M	5.2	60.4
40	6	11	M	6.2	67.0
15.5	6	11	M	4.9	57.6
90.5	5	26	M	5.6	64.9
26.5	5	12	M	5.2	60.4
37	17	25	F	4.6	61.1
31	14	20	F	4.3	59.2
17	5	13	F	4.3	62.9
15.5	5	5	F	4.1	59.9

HRA (Rose, 1982; Stamps, 1983; Christian & Waldschmidt, 1984). All of these predictions were met by these data. Interval of recapture had the strongest correlation with log HRA ( $r = 0.786$ ), but log body mass ( $r = 0.479$ ), number of captures ( $r = 0.611$ ), and sex (males = 1,  $r = 0.412$ ) were also positively correlated. The regression model which best fit the 21 individuals captured five or more times was as follows:

$$\log HRA = 0.106 + 1.260 \times \log \text{body mass} + 0.030 \times \text{interval}$$

The overall model was highly statistically significant ( $R^2 = .739$ ;  $F_{2,18} = 25.53$ ;  $P < .0001$ ; standard error of estimate = 0.180), and both log body mass (partial  $F = 8.45$ ;  $P < 0.01$ ) and interval of recapture (partial  $F = 35.23$ ;  $P < 0.001$ ) were significant predictors of HRA. Neither number of recaptures (partial  $F$  to enter = 0.08;  $P > 0.5$ ) nor sex (partial  $F$  to enter = 0.03;  $P > 0.5$ ) added significantly to the model. We then used the average log body mass of the 17 males (0.782) and of the four females (0.636) along with the maximum number of days between first and last recapture (34) to estimate HRA. We used the maximum value for the interval because we felt that many of the individual lizards were caught an insufficient number of times to accurately estimate HRA (Schoener, 1981), and we did not want to underestimate HRA. Using the foregoing values we estimated a log HRA of 2.11

(antilog = 132.3 m<sup>2</sup>; 95% CI = 54.1 - 306.9 m<sup>2</sup>) for males and of 1.93 (antilog = 86.5 m<sup>2</sup>; 95% CI = 35.7 - 202.8 m<sup>2</sup>) for females.

Our HRA estimate for male *P. h. atrata* (132.3 m<sup>2</sup>) is slightly larger than that reported for conspecifics from the mainland (*Podarcis hispanica hispanica*) during the same month (mean = 120.0 m<sup>2</sup>; Gil, Pérez-Melado & Guerrero, 1988). Our HRA estimate for female *P. h. atrata* (mean = 86.5 m<sup>2</sup>) is considerably larger than reported for females from the mainland (29.1 m<sup>2</sup>; Gil *et al.*, 1988). Adult *P. h. hispanica* are considerably smaller (adult males = 3.0 g; adult females = 2.8 g; Castilla, unpublished) than adult *P. h. atrata*. In any case, comparisons between these two populations are problematic because of differences in methodology and body mass. Furthermore, caution should be taken when making claims from comparisons that involve only two species or subspecies (Garland & Adolph 1994).

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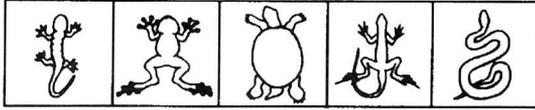
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