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FRONT COVER: Juvenile natterjack toads, Bufo calamita (P. Benson)

A NEW SPECIES OF THE WESTERN INDIAN OCEAN GECKO AILURONYX (REPTILIA; GEKKONIDAE)

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A new species of gecko of the genus *Ailuronyx* is described from the Seychelles islands of Mahé and Praslin. This species, *Ailuronyx tachyscopaeus*, differs from previously described species in being smaller, having fewer femoro-anal pores in the males and distinct squamation. Some ecological observations are made concluding that the species is locally abundant in native palm forest.

INTRODUCTION

The genus *Ailuronyx* is recorded from the Seychelles islands and Madagascar. Two species have been described previously: the type species *A. seychellensis* (Duméril & Bibron, 1836) from several of the Seychelles islands and *A. trachygaster* (Duméril & Bibron, 1851) which is known only from the holotype. The provenance information for the latter is "Madagascar"; collection data are lacking and it is possible that Madagascar may have been its port of shipment to Paris rather than its collection locality (Bauer, 1990; Ineich *pers. comm.*). Thus the genus may be endemic to the Seychelles islands.

Since the original description of the genus there have been few published studies of it. A small number have included the genus in broader taxonomic studies (Russell, 1972) and there have been some preliminary ecological investigations (Cheke, 1984; Evans & Evans, 1980; Henkel & Zobel, 1987). The most detailed of these (Henkel & Zobel, 1987) included observations of both wild and captive geckos, and suggested that up to three species may be present in the Seychelles. A karyological study of two colour morphs failed to demonstrate specific differences (Volobouev & Ineich, 1994).

In 1993 several small *Ailuronyx* were observed in a house at Anse Royale, Mahé by M. Kirkpatrick. This is an unusual habitat for the genus on Mahé (although it is frequently anthropophilic on Fregate, Praslin and Aride, *pers. obs.*). One was caught on 1 January 1994 and photographed. Subsequent comparisons with specimens in the British Museum (Natural History) suggested that it was not a typical *A. seychellensis.* The photographs appeared to resemble the dwarf form described by Henkel & Zobel (1987). In July 1994 searches were made for this dwarf form at La Reserve, Mahé, where small *Ailuronyx* had been observed in previous years. Five specimens were caught, measured and kept for four weeks, one of these was preserved, the others released. A number of 'dwarf' specimens were

also observed in the Vallée de Mai, Praslin, where the dwarf form had been reported (Henkel & Zobel, 1987). Comparisons were made with *A. seychellensis* revealing differences that led to the conclusion that the dwarf form should be regarded as a distinct species. The differences between the species are discussed and the two Seychelles species described below.

MATERIALS AND METHODS

A number of characters were recorded and compared with specimens of A. seychellensis in the British Museum (Natural History) and the Muséum national d'Histoire naturelle, Paris. The characters used were measurements of snout-vent length, snout length (the distance between the tip of the snout and the anterior margin of the eye), eye diameter, eye-ear distance (between the posterior margin of the eye and the anterior margin of the ear), head width and counts of the number of supra-ocular spines, upper and lower labials, femoro-anal pores and lamellae on the 4th toe of the right hind foot. Lamellae were defined as scales that were at least twice as long as wide. For labials, all scales along the mouth edge that were distinct from granular scales were included. In addition, the squamation was examined under a binocular microscope on preserved museum specimens and on skin fragments from museum specimens and from the live collected individuals.

MEASUREMENTS

No significant measurement differences were detected between the two forms or any of the island populations using *t*-tests of the data collected.

COUNTS

The numbers of upper and lower labials, lamellae and femoro-anal pores were compared to snout-vent length using Pearson's correlation coefficients. No significant correlations were found (P>0.1 in all cases) indicating that these counts do not change with growth.

t-tests comparing data from A. seychellensis and the 'dwarf' specimens were performed on the counts of lamellae, labials and femoro-anal pores. Significant differences were found in the number of upper labials $('dwarf' = 15.6 \pm 0.2, A. seychellensis = 17.2 \pm 0.7,$ t=2.66, P=0.011); and femoro-anal pores ('dwarf' = 14.8±1.3, A. seychellensis = 23.9±5.2, t=8.32, P=0.001). This difference in counts of femoro-anal pores could indicate either that the 'dwarf' and typical forms represent different taxa or that the 'dwarf' form is a sub-adult stage. In order to distinguish between these possibilities the femoro-anal pores of the captive males were examined daily to determine whether or not pore development was complete. Two specimens had fully developed continuous rows of 15-16 large, darkly pigmented pores on capture, the number of pores remained constant during the period of observation. The remaining male lacked any detectable pores when collected but had a continuous row of 15 pores when released. These developed from the centre and edges of the row. A week before the specimen was released new pores stopped developing (all gaps in the row having been filled) and dark pigmentation appeared. This pattern of development suggests that maturity in 'dwarf' males is reached at a snout-vent length of approximately 68 mm. A female of 76 mm snout-vent length had obvious enlarged endolymphatic sacs confirming that these are not immature A. seychellensis. Sexual maturity of the 'dwarf' form is further demonstrated by the captive reproduction recorded by Henkel & Zobel (1987).

SQUAMATION

Significant differences were apparent between the two forms. The 'dwarf' was noticeably smoother skinned than equivalent sized *A. seychellensis* demonstrating that this difference is not explicable by ontogenetic processes although some minor squamation differences were detectable between juvenile and adult *A. seychellensis*. Scales from the backs and tails of adult and juvenile *A. seychellensis* and from a 'dwarf' are shown in Fig. 2. These are described in full in the descriptions below.

Museum specimens allowed comparisons to be made between individuals from a number of islands (Aride, Cousin, Cousine, Fregate, Mahé, Praslin and Silhouette). No significant differences could be found between the island samples using t-tests of the characters described above. 'Dwarf' specimens were identifiable in Mahé and Praslin samples based on the squamation differences described above. Museum specimens of A. seychellensis covered a broad ontogerange, allowing the separation netic of phylogenetically significant characters from those related to development.

These comparisons demonstrate that two forms of Ailuronyx are recognisable in Seychelles. One of these corresponds to the species A. seychellensis and is found on many islands. No significant morphological variation is detectable between islands. The second form has previously been recorded as a 'dwarf' form (Henkel & Zobel, 1987). This is present on at least two islands (Mahé and Praslin) where it coexists with A. seychellensis (Henkel & Zobel, 1987; pers. obs.). The consistent differences in squamation and scale counts indicate that this 'dwarf' form is taxonomically distinct from A. sevchellensis; its presence on two islands and its sympatric occurence with A. seychellensis demonstrate that the two forms are not merely local variants and are distinct at the species level. Accordingly the 'dwarf' form is described below, following a full description of the type species of the genus, A. seychellensis.

SPECIES DESCRIPTIONS

Genus

Ailuronyx Fitzinger, 1843

TYPE SPECIES

Ailuronyx seychellensis (Duméril & Bibron, 1836)

DIAGNOSIS

Predominantly nocturnal geckos with granular dorsal scales; supra-ocular spines usually present. Pupil vertical. Lamellae on toepads undivided; a large claw is present on each digit, claws asymmetrically positioned. Femoro-anal pores and hemipenial pouches present in males; cloacal spurs may be present in large specimens.

Ailuronyx seychellensis (Duméril & Bibron, 1836) Platydactylus Seychellensis Duméril & Bibron, 1836: 310

Thecodactylus (Ailuronyx) sechellensis Fitzinger 1843: 19

Teconyx sechellensis Gray 1845: 159 Aeluronix seychellensis Agassiz 1846: 9

Ailuronyx seychellensis Rendahl 1939; 257

SYNTYPES

Two adult male syntypes in the Muséum national d'Histoire naturelle, Paris (MNHN 2269 & 6677). Collected by Péron & Lesueur; locality given as Seychelles without further details. Described by Duméril & Bibron (1836).

MATERIAL STUDIED

Forty-one specimens in the British Museum (Natural History) and 12 in the Muséum national d'Histoire naturelle, Paris.

NEW GECKO SPECIES

A. seychellensis	Range	Mean	SD	п	Syntype MNHN 2269	Syntype MNHN 6677
Snout-vent length	81-116	101.5	7.6	53	111	114
Head length	18-31	26.1	3.2	53	24	25
Head width	17-25	21.5	1.8	53	22	24
Snout length	8-14	11.9	1.5	53	10	11
Eye diameter	4-7	5.3	0.8	53	6	6
Eye-ear distance	6-10	7.9	0.9	53	8	8
Snout angle	30-42	40.5	0.5	53	42	40
Upper labials	12-19	15.2	0.8	53	15	15
Lower labials	12-16	13.5	0.9	53	13	13
Postmental number	7-9	8.5	0.3	53	9	8
A. tachyscopaeus	Range	Mean	SD	п	Holotype MNHN 1994.3109	Paratype BMNH 1907.10.15.54
Snout-vent length	56-84	69.2	9.1	7	68	84
Head length	13-20	17.8	2.5	7	18	19
Head width	12-18	14.9	2.2	7	14	16
Snout length	6-10	8.7	1.5	7	9	10
Snout length Eye diameter	6-10 3-4	8.7 3.9	1.5 0.4	7 7	9 4	10 4
Snout length Eye diameter Eye-ear distance	6-10 3-4 4-6	8.7 3.9 5.0	1.5 0.4 0.6	7 7 7	9 4 5	10 4 5
Snout length Eye diameter Eye-ear distance Snout angle	6-10 3-4 4-6 15-25	8.7 3.9 5.0 20.0	1.5 0.4 0.6 4.0	7 7 7 7	9 4 5 18	10 4 5 20
Snout length Eye diameter Eye-ear distance Snout angle Upper labials	6-10 3-4 4-6 15-25 15-19	8.7 3.9 5.0 20.0 18.2	1.5 0.4 0.6 4.0 0.5	7 7 7 7 7	9 4 5 18 18	10 4 5 20 18
Snout length Eye diameter Eye-ear distance Snout angle Upper labials Lower labials	6-10 3-4 4-6 15-25 15-19 13-19	8.7 3.9 5.0 20.0 18.2 17.0	1.5 0.4 0.6 4.0 0.5 0.3	7 7 7 7 7 7 7	9 4 5 18 18 18 16	10 4 5 20 18 17

TABLE 1. Morphometric data of Ailuronyx spp.

DISTRIBUTION

Endemic to Seychelles; Mahé, Praslin, Aride, Cousin, Cousine, Silhouette, Fregate.

DIAGNOSIS

Large adult size (up to 116 mm snout-vent length); rostral contacts nostril; snout descending steeply; body covered with conical granular scales, rough in appearance; caudal scales regular, pentagonal, with longitudinal ridges on their posterior edges; 20-34 femoro-anal pores.

DESCRIPTION

Measurements, body and squamation. Measurements are given in Table 1. The snout descends rapidly, forming an angle of almost 45° with the lower jaw (range = $30-42^{\circ}$). The rostral always contacts the nostril, which is contacted at its anterior border by the rostral, nasal, supranasal and postnasal (Fig. 1.). Upper labials number 12-19 and lower labials 12-16. The mental is pentagonal and equal in size to the adjacent

labials. There are 7-9 postmentals. These data are summarised in Table 1.

The scales on the head, dorsal surface of the body and limbs are granular, those on the tail and ventral surfaces flat and angled posteriorly. On the head the scales are small (approximately 0.3 mm wide in adults) and conical, irregular in size and arrangement. Those on the back are larger and more elevated (up to 1.2 mm wide and 1.4 mm high in adults). On the midline of the body the scales are regularly arranged, trapezoid in basal section and slightly depressed on the posterior facets, resulting in their projecting backwards. This regularity is also found on the scales of the limbs which are smaller and do not project backwards. All granular scales have a regular ornamentation of fine radial ridges, at a density of approximately 32 mm⁻¹. Juvenile specimens lack the regular arrangement on the midline but share the arrangement and density of ridges. The tail and underside have regularly arranged pentagonal flat scales, those on the underside being smooth whereas the tail scales are ornamented with six longitudinal ridges on the posterior margin. The scales



FIG. 1. Heads of Seychelles Ailuronyx. A, A. seychellensis (MNHN6677). Scale bar = 40 mm. B, A. tachyscopaeus (MNHN1994.3109). Scale bar = 20 mm. C, A. seychellensis showing arrangement of scales on the snout (r = rostral). D, A. tachyscopaeus showing arrangement of scales on the snout (r = rostral).



FIG. 2. Scales of Seychelles *Ailuronyx*. A, *A. seychellensis* (adult) - dorsal mid-line scales in dorsal, lateral and anterior views. B, *A. seychellensis* (juvenile) - dorsal mid-line scales in dorsal, lateral and anterior views. C, *A. tachyscopaeus* (adult) - dorsal mid-line scales in dorsal, lateral and anterior views. D, *A. seychellensis* - tail scales. E, *A. tachyscopaeus* - tail scales. Scale bar = 1mm.

on the base of the tail of adult specimens are up to 0.9 mm wide, 0.8 mm long at the margins and 0.9 mm long at the centre. One to seven supra-orbital spines are present above each eye in some specimens (41.5% of those examined lack spines; if spines were present they numbered on average 3.3); on average these are 0.9 mm long, but they may approach 2 mm. There are 20-28 lamellae on the 4th right hind toe. Femoro-anal pores are present in adult males only, numbering 20-34 (mean = 23.9 ± 5.2). The smallest individuals with detectable femoro-anal pores had a snout-vent length of 73 mm. Fully developed pores were not observed in specimens below 95 mm snout-vent length. A single pair of cloacal spurs is present in some males.

Colouration. Two colour patterns are apparent; one is a pale fawn colour with paler speckling, the other is a complex pattern of dark brown, fawn and white spots. A pale band along each side of the head is visible in both forms. These two patterns are exhibited by the same individual, the pale colour being the normal pattern and the darker corresponding to the alarm pattern described by Henkel & Zobel (1987). The two patterns are shown in Fig. 1., where (A) (A. seychellensis syntype) exhibits the normal patterning and (B) ('dwarf' form) exhibits the alarm pattern. The conspecificity of specimens with different colour patterns (and hence their lack of phylogenetic significance) has been confirmed from karyological data (Volobouev & Ineich, 1994).

Ailuronyx tachyscopaeus sp. nov.

HOLOTYPE

Holotype in the Muséum national d'Histoire naturelle, Paris (MNHN 1994.3109); caught at La Reserve, Mahé 26/6/94, died in captivity 13/7/94 - adult male.

PARATYPE

Paratype in the British Museum (Natural History) (BMNH1907.10.15.54); collected at Anse Marie Louise, Praslin by the Percy Sladen Memorial Expedition 1907 - adult male.

MATERIAL STUDIED

One specimen caught and released at Anse Royale, Mahé 1/1/93. Five specimens, including holotype, caught (all released except for holotype) at La Reserve, Mahé 26/6/94 & 23/7/94. One specimen (paratype) in the British Museum (Natural History) (BMNH 1907.10.15.54). In addition nine specimens were observed but not caught at La Reserve, Mahé, 23/7/94 and Vallée de Mai, Praslin 27/7/94.

DISTRIBUTION

Identity confirmed on Mahé (La Reserve, Anse Royale) and Praslin (Vallée de Mai, Anse Marie Louise).

DIAGNOSIS

Small adult size (up to 84 mm snout-vent length); rostral not contacting nostril; snout tapering gradually; granular scales, small low cones; caudal scales regular, smooth with curved posterior margins; five supraorbital spines, the third directed posteriorly; 13-16 femoro-anal pores.

ETYMOLOGY

The specific name *tachyscopaeus* is a composite of *tachys* (Greek for swift) and *scopaeus* (Latinization of the Greek *skopaios*, meaning dwarf). This refers to the rapid movements and agility of the species in comparison to the more inactive *A. seychellensis* and to its original identification as a dwarf form of that species.

DESCRIPTION

Measurements, body and squamation. Measurements are given in Table 1. The snout tapers gradually, its angle with the lower jaw not exceeding 25° (range = $15-25^{\circ}$). There are 15-19 upper labials and 13-19 lower labials. The rostral does not contact the nostril, which is bounded on its anterior border by the nasal, supranasal and post-nasal (Fig. 1.). The mental is pentagonal in shape and equal in size to the adjacent labials. There are nine postmentals. These data are compared to *A. seychellensis* in Table 1.

As in A. seychellensis the scales on the head, dorsal surface of the body and limbs are granular and those on the tail and ventral surfaces are flat and cvcloid. The scales on the head are small (less than 0.25 mm wide) and conical, irregular in size and arrangement. Those on the back are distinctly flatter than those of A. seychellensis (being at most only 0.3 mm high, compared with 1.4 mm and 0.8 mm in adults and juveniles of the former species respectively). There are no regions with regular granular scales. The ridges on the granular scales are less dense than they are on A. seychellensis, numbering fewer than 12 mm⁻¹. The tail and underside have regularly arranged pentagonal flat scales with curved posterior margins; all are smooth. The scales on the base of the tail are equal in width to those of A. seychellensis (0.9 mm) but are shorter, being only 0.6 mm at the longest point. The number and arrangement of supra-orbital spines appears to be highly conservative in this species. All the specimens examined possessed five spines, the third of which is posteriorly directed. At their longest the spines measure 0.42 mm; up to two of the spines may be only 0.1mm long and are hard to detect. There are 20-24 lamellae on the 4th right hind toe. All the digits are terminally expanded and clawed. Femoro-anal pores are present in adult males only, numbering 13-16 (mean = 14.8 ± 1.3 , n=5). The smallest male caught (61) mm snout-vent length) had detectable femoro-anal pores. Fully developed pores were only found in males

over 68 mm snout-vent length. No cloacal spurs have been observed.

Colouration. The colour patterns of A. seychellensis are also found in A. tachyscopaeus.

SUMMARY OF DIFFERENCES

A. tachyscopaeus differs from A. seychellensis in its smaller adult size, less steeply angled snout, the rostral not contacting the nostril, the flatter and smoother squamation, the cycloid shape of the ventral and tail scales and the lower number of femoro-anal pores. These differences are constant and cannot be attributed to ontogenetic, sexual or geographical factors.

ECOLOGICAL NOTES

The surveys undertaken in June-July 1994 involved the collection of live specimens and the counting of all individuals along transect lines. Specimens caught were identified using the diagnostic characters in the species descriptions. Other specimens were examined closely and identified on the basis of the smoothness or roughness of the scales. In most cases the geckos could be approached closely enough to be examined with a hand-lens even if they eventually evaded capture. At La Reserve on Mahé only A. tachyscopaeus were found; these were in the partially rolled-up leaves of the palm-like hypoxidacean shrub Curculigo sechellensis. The species had previously been encountered at the same site between hanging dead leaves of the palm Phoenicophorium borsigianum. A total of nine were found in eight clumps of C. sechellensis (or 42% of the clumps along a 100 x 2.5 m transect), giving a density of 400 per hectare. This may be an under-estimate as it does not include individuals living in the palm leaves overhead. On Praslin $C_{\rm c}$ sechellensis is uncommon and all Ailuronyx were seen on the trunks and leaves of the palm Lodoicea maldivica. Only five (four A. tachyscopaeus and one A. seychellensis) were seen along a 1900 x 6 m transect, giving a density of 0.9 per hectare for A. seychellensis and 3.4 for A. tachyscopaeus. The transect method does not provide reliable estimates in this habitat, due to the vegetation structure.

Previous reports have claimed that *Ailuronyx* are rare on Mahé (Evans & Evans, 1980; Cheke, 1984; Gardner, 1986), this study demonstrates that they are locally abundant in areas of suitable palm forest. However, it should be noted that this habitat type is very restricted on Mahé. These data, and the recent rediscovery of *A. seychellensis* at four different localities on Silhouette (*pers. obs.*; Gerlach 1993; Oxford University Silhouette Expedition 1990; Matyot *pers. comm.*) where it had been believed to be extinct (Cheke, 1984; Gardner 1986), suggest that *Ailuronyx* spp. are dependent on palm forest on the larger islands and that the restriction of this habitat has resulted in their being overlooked on Mahé and Silhouette, rather than that they have declined as a result of the introductions of rats (*Rattus rattus*, *R. norvegicus*) or tenrecs (*Tenrec ecaudatus*).

Observations on captive A. tachyscopaeus show that, like A. seychellensis, it is predominantly, although not exclusively, nocturnal. The behaviour of "alarm skin-shedding" (Bauer et al., 1989; Evans & Evans, 1980; Henkel & Zobel, 1987; McKeown & Miller, 1985) is found in both species. Captive A. tachyscopaeus consumed moths and a large earwig but refused a variety of large and small dipteran flies.

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DISTRIBUTION OF SCHREIBER'S GREEN LIZARD (*LACERTA SCHREIBERI*) IN PORTUGAL: A PREDICTIVE MODEL

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The geographic distribution of the endemic Iberian lizard *Lacerta schreiberi* in Portugal was determined through extensive field surveys. Subsequently, a logistic regression model which predicts the probability of occurrence, based on environmental variables, was developed. We found that *L. schreiberi* is more widely distributed than previously thought, through most of central/northern Portugal, including the coastal zone and extending into low altitude zones. New isolated populations were also detected and the area occupied by three previously known southern isolates was enlarged. The model indicates that the distribution of *L. schreiberi* is largely explained by environmental parameters such as insolation, evapotranspiration, rain, humidity and soil-drainage. Values of probability of occurrence greater than 0.50, as determined by our model, correspond with the actual presence of the species.

INTRODUCTION

Lacerta schreiberi is a medium-sized lizard (adult snout-vent-length 117-120 mm), endemic to the Iberian Peninsula. It exhibits a pronounced sexual dimorphism, the adult males being smaller than the females and having an intense blue coloration on the head during the mating season (Barbadillo, 1987). It usually occupies mountain regions (up to 2100 m) and their surroundings, but may also be found at low altitudes if suitable conditions occur (Marco & Pollo, 1993). L. schreiberi inhabits relatively high humidity locations, mostly water courses, with dense vegetation cover. It is a good climber of stone walls and bushes (Brito, 1994), and feeds mostly on Coleoptera, Formicidae and Diptera (Marco & Pérez-Mellado, 1988).

L. schreiberi has a marked Atlantic distribution, occurring in Spain in Galicia, Cantábria, Northern Castilla-León, Central Range Mountains (Sistema Central) and also in several isolated populations in the south (De La Riva, 1987; Marco & Pollo, 1993) (Fig. 1). In Portugal, it occurs in the northern half of the country and in three known isolated populations in the south: Serra de S. Mamede, Serra de Sintra and Serra de Monchique (Malkmus, 1981; Crespo & Oliveira, 1989; Malkmus, 1995) (Fig. 1).

Our work was conducted as part of a project on the conservation of *L. schreiberi* in Portugal, under guidelines of the European Union LIFE Program. The two aims were (1) to describe through field surveys the distribution of the species in Portugal, and (2) to derive a predictive model for the distribution, using logistic regression, in order to evaluate the probability of occurrence of the species in any given area.

Logistic regression is a tool for analysing the effects of one or several independent variables, discrete or continuous, on one dependent polychotomous variable (e.g., presence/absence). It has been used recently for modelling wildlife distributions (Walker, 1990) and abundance (Gates, Gibbons, Lack & Fuller, 1994). A logistic regression has the form: $\pi(x) = e^{g(x)} / (1 + e^{g(x)})$, where *e* is the base of the Naperian logarithm and $\pi(x)$ is the probability of occurrence of the species, ranging from 0 to 1. The value of g(x) is obtained by a regression equation of the form: $g(x) = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + ... + \beta_p x_p$ where β_0 is a constant and $\beta_1 ... \beta_p$ are the coefficients of the $x_1 ... x_p$ independent variables. A multivariate logistic regression model, based on environmental variables, was used to predict the probability of occurrence of *L. schreiberi* in all of the Portuguese UTM (Universal Transverse of Mercator grid) l0x10 km cells.



FIG. 1. Previously known distribution of *L. schreiberi* in the Iberian Peninsula. A, Serra de Sintra; B, Serra de S. Mamede; C, Serra de Monchique; D, Sierra de Ias Villuercas; E, Montes de Toledo; F, Sierra de San Andrés. Shaded: known area; vertical hatching: possible occurrences; arrows: possible ancient connection passages (Modified from De La Riva, 1987).

MATERIAL AND METHODS

DISTRIBUTION

The field sampling strategy for surveys was based on two criteria: first, the previously known distribution according to Malkmus (1981, 1995) and Crespo & Oliveira (1989), but instead of reconfirming this distribution we opted for trying to delimit the areas in which the lizard was present. Second, we sought to determine the potential areas of occurrence, which included habiwhere the environmental characteristics. tats considered important by Marco & Pollo (1993) (e.g. annual rainfall above 800 mm), are favourable for L. schreiberi. These characteristics were obtained from the Portuguese Environmental Atlas (C.N.A., 1983). The field work was conducted between March and September 1994, and covered most of the northern/central Portuguese territory and also the southern regions where isolates are known or where areas of potential occurrence exist, in a total area of approximately 31000 km². In total, 470 rivers and streams were sampled. At each, two observers diverged in opposite directions from a common starting point, and walked for about 20 min., visually detecting lizards within the water margins. The known information on the distribution was compiled in a database and represented through occurrence points in a UTM l0x10 km grid, which was later updated with our results.

LOGISTIC REGRESSION

A matrix was built with information on presence/ absence of the species (dependent variable) in 422 UTM I0x10 km cells. Each cell was assigned values for the following independent variables, thought to be relevant, and grouped in classes (Appendix 1): number of hours of sun per year (*insolation*); mean daily temperature (*temperature*); total rain in mm per year (*rain*), relative humidity at 9.00 G.M.T. (*humidity*); amount of water in the streams (*soil drainage*); amount of water returned to the atmosphere (*evapotranspiration*); altitude; type of soil (*soil*); phytoedapho-climatic information (*ecology*); number of humans/km² (*human population density*).

From the initial set of cells we chose two random subsamples. One subsample, with 362 cells, was used to build and assess the fit of the model. The other, the validation subsample, with 60 cells, was used only to evaluate the accuracy of the predictions of the final model. To determine the regression model, we used the software Egret (1991) and followed the procedure of building and evaluating multivariate logistic regressions suggested by Hosmer & Lemeshow (1989).

UNIVARIATE ANALYSIS

Univariate logistic regression analysis indicates whether there is any association between each environmental variable and the binary dependent variable. The selection of the relevant independent variables was performed using the maximum likelihood ratio test (G test) and the Wald test (Hosmer & Lemeshow, 1989). Any variable for which the Wald test had a P < 0.25 was considered for inclusion in the multivariate model.

MULTIVARIATE ANALYSIS

Once the variables were selected by univariate analysis, they were included in a preliminary model and in a backward elimination procedure those with P >0.25 and those whose Odds ratio estimation (95% confidence) included the value 1 were eliminated. The Odds ratio is a measure of association which approximates how much more likely (or unlikely) it is for the outcome to be present among those with x=1 than among those with x=0 (Hosmer & Lemeshow, 1989). For example, if y denotes the presence/absence of a species and if x denotes a binary independent variable, then an Odds ratio of 2 indicates that the species occurs twice as often among the places with the variable equal to one than among those with value zero. In continuous variables we have to develop a method for point and interval estimation for an arbitrary change of c units in the variable. The Odds ratio for a change of c units of the variable x is obtained through: $\Psi(c) = \exp(\frac{1}{2}) \exp(\frac{1}{2})$ $(c\beta_{1})$, being β_{1} the coefficient for the variable x. Hence, variables are rejected when their Odds ratio estimation (95% confidence) include the value 1, which denotes a low level of association between the variable and the presence/absence of the species (Hosmer & Lemeshow, 1989).

LINEARITY

Continuous variables were checked for linearity, by two methods. Adding the Box-Tidwell transformation $(x.\ln x)$ to the model, resulting in evidence of non-linearity if the values of the *P* and *G* tests for this new variable were significant. The other method involved fitting the square and log transformations of each variable and performing a univariate analysis with these new variables. If the *G* test or the Wald tests were significant the transformed variable was included in the model and used in subsequent analyses (see Hosmer & Lemeshow, 1989; and Gates *et al.*, 1994, for technical details).

CONFOUNDED VARIABLES AND INTERACTIONS

Any confounded variables were assessed by adding all the initial variables, one after the other, to the model and simultaneously checking the effect of the added variable on the estimated coefficients of the variables that were already in the model, and on the G test. Confounded effects were significant when an increment of the G test value or its significance was observed. Interactions were added to the model, derived from the previous analysis, by creating a new variable which is equal to the product of the value of two variables. Again, interactions were significant if an increment of the G test value or its significance was observed, and if so they were included in the model (see Hosmer & Lemeshow (1989) for technical details).

ASSESSING THE FIT OF THE MODEL

To assess the fit of the model we used the Pearson chi-square and a classification table (Hosmer & Lemeshow, 1989). The Pearson chi-square was calculated as indicated below:

$$X^{2} = \sum_{j=1}^{n} (y_{j}, \pi_{j})^{2}$$
where $r(y_{j}, \pi_{j}) = \frac{(y_{j} - \pi_{j})}{(\pi_{j}(1 - \pi_{j}))^{0.5}}$
where $r(y_{j}, \pi_{j}) = \frac{(y_{j} - \pi_{j})}{(y_{j}, \pi_{j})^{0.5}}$

The classification table considered the observed value of the dependent variable, the presence or absence of the species, and the predicted value of presence or absence as a function of the estimated probability of occurrence based on the multivariate model. To generate the table, it was necessary to set a cut-off point, the probability value above which we consider that the species is present. We follow the recommended cut-off point of 0.30 suggested by Walker (1990) for this kind of analysis.

RESULTS AND DISCUSSION

DISTRIBUTION

Fig. 2 presents the new sites of occurrence found during our field work together with those previously known. Expansion of the geographic distribution is evident in three cases. First, there is an extension to all the littoral strips, to the north of the river Tagus, including zones of high human pressure (urbanization



FIG. 2. Updating of the distribution area of *L. schreiberi* in Portugal with new sites detected in this work. A, Serra de Sintra; B, Serra de S. Mamede; C, Serra de Monchique; D, Serra de Montejunto; E, Serra do Cercal (Grid: UTM $10 \times 10 \text{ km}$).

FIG. 3. Probability of occurrence of *L. schreiberi* in Portugal following the model defined (each circle represents the probability of a UTM 10×10 km cell).

and industries). In this coastal area, the presence of *L. schreiberi* is frequent in marshes where the vegetation cover is of reed (*Arundo donax*) and slender reed (*Phragmites* sp.) (Brito *et al.*, 1994). This habitat has not been previously considered as suitable for this species.

Second, for central/northern Portugal, the occurrence of *L. schreiberi* was only known for areas of relatively high altitude (cf. Crespo & Oliveira, 1989; Malkmus, 1995). Our work has shown that the distribution is continuous for this region rather than restricted to mountains, with an exception for part of the north-eastern region and the more interior part of the River Douro. These exceptions are probably due to climatic constraints (see below).

Thirdly, the area occupied by the known isolated populations in the south (Sintra, S. Mamede and Monchique) has proved to be wider than previously reported (Malkmus 1981, 1995; Crespo & Oliveira, 1989). In addition, two new isolates were detected: near Serra de Montejunto, in the region of Estremadura, and in Serra do Cercal, Alentejo (Fig. 2). Although the possibility of a connection between the Sintra and Montejunto isolates with the northern area was considered, later field work could not confirm this. The reduced number of individuals detected in these two new isolates, and also in the isolate of Serra de Sintra, leads us to believe that these are very small populations and may be facing extinction.

The general enlargement of the distribution of *L. schreiberi* in Portugal is, in our view, the result of a lack of extensive sampling in the past, and not to a subsequent expansion of the species.

LOGISTIC REGRESSION

Although six models were produced, we only present one because this explains significantly more variation than all the others. For this model, in the univariate analysis we eliminated the variables *population density* and *soil*, and in the multivariate analysis, the variables *temperature*, *altitude* and *ecology* were also eliminated. No confounded effects were detected but interactions appeared between *insolation* and *evapotranspiration* and between *rain* and *humidity*. Although *temperature* and *humidity* showed evidence of non-linearity, the inclusion of the transformed variables resulted in a regression model with less statistical power. The resulting regression equation is as follows:

g(x)= -5.001- 0.04028 (insolation x evapotranspiration) + 0.104 (rain x humidity) + 0.7023 (soil draining)

The model agrees closely with the observed values. The Pearson chi-square ($X^2_{0.05,356} = 374.97$) and the classification table (75% of presences were classified as presence; 94% of absences were classified as ab-

sence and 82% of the cells were correctly classified) suggests that the model is a good predictor of the distribution of L. schreiberi. The validation sample gave inferior chi-square values and percentages (X² 0.001 54 83.89, 56% of presences were classified as presence; 96% of absence were classified as absence and 72% of the cells were correctly classified). The model explains absence of the species much better than presence. The smaller value obtained by the "presence classification" is due to the fact that the model only considers climatic variables as determinants for the distribution. In reality, climate is not the only factor determining L. schreiberi distribution. For example, other habitat characteristics may be unsuitable in areas which are climatically ideal for the species. This is especially evident in the littoral areas (cf. Fig. 3 with Fig. 2) where the climatic conditions are favourable but the habitat is widely disturbed, so although the model produces a high score for these areas L. schreiberi is frequently absent. Future research should aim at improving the model by incorporating other relevant variables, such as descriptors of habitat quality. The results could also be improved either by changing the scale to a more precise one or by using different modelling approaches, namely by using different sets of random cells in order to deal with spatial autocorrelation.

The probability of occurrence of *L. schreiberi* in Portugal in presented in Fig. 3. The null probability for the inner Douro River and north-eastern region confirms the climatic unsuitability of this area for this species. Above the 0.50 probability of occurrence, the presence of the species is frequent (cf. Fig. 2). The map of probabilities also gives some clues for further research on this species.

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class	insolation evapotranspira (hrs/yr) (mm/yr)		rain (mm/yr)	humidity (%)	soil drainage (mm)
1	<1900	<350	<400	<65	<25
2	1900-2000	350-400	400-500	65-70	25-50
3	2000-2100	400-450	500-600	70-75	50-100
4	2100-2200	450-500	600-700	75-80	100-150
5	2200-2300	500-600	700-800	80-85	150-200
6	2300-2400	600-700	800-1000	>85	200-300
7	2400-2500	700-800	1000-1200	-	300-400
8	2500-2600	>800	1200-1400	-	400-600
9	2600-2700	-	1400-1600	-	600-800
10	2700-2800	-	1600-2000	-	800-1000
11	2800-2900	-	2000-2400	-	1000-1400
12	2900-3000	-	2400-2800	-	1400-1800
13	3000-3100	-	>2800	-	1800-2200
14	>3100	-	-	-	>2200

APPENDIX 1. Classes of the environmental variables used in the regression equation

HABITAT OCCUPANCY BY JUVENILE NATTERJACK TOADS (*BUFO CALAMITA*) ON GRAZED AND UNGRAZED HEATHLAND

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Habitat utilization by natterjack toads (*Bufo calamita*) during their first two years of life was investigated using a series of replicated 20 x 20 metre squares demarcated on several distinctive habitat types on a heathland in southern England. Two sets of squares, one on ungrazed heathland and one in an area grazed at low density by domestic cattle, were employed and the fate of toadlets released on the squares monitored over three successive years. Habitat use by resident adult natterjacks, and common toads *B. bufo*, was also recorded as was habitat selection over the site as a whole outside the experimental squares. Although toadlet survival was apparently low (though it was not possible to distinguish mortality from emigration), this and habitat selection by adults were unaffected by the presence of livestock. Juvenile natterjacks utilised the same range of habitats as adults, but the former showed greater preference for damp pond basins and rather less for dry bryophytes compared with mature animals. Common toads were rare in all habitats favoured by natterjacks, but were more often found in ungrazed rather than in grazed terrain.

INTRODUCTION

The juvenile life of pond-breeding amphibians between metamorphosis and sexual maturity is notoriously difficult to study but is probably of considerable importance with respect to population dynamics. Mortality rates, though usually lower than those of aquatic larvae, are high by comparison with adults in most species (e.g. Beebee, 1996). It is also a time at which selection may operate strongly, and genotype frequencies in Bufo boreas, for example, change significantly during early growth (Samollow, 1980). Juvenile B. calamita behave differently from adults at least during their first summer of life, being largely diurnal in Britain despite the problem of water conservation consequent upon a high surface area: volume ratio, and without the physical strength required to dig deep burrows (Beebee, 1983). This might mean that toadlets require special habitats in order to survive, and in this study we set out to investigate this aspect of toadlet ecology. We also wanted to determine whether grazing heathland with low densities of domestic animals, an increasingly popular management method, affected survival or habitat occupancy of both juvenile and adult natterjacks.

METHODS

The study was carried out at Woolmer Forest, a lowland heath in southern England with a small natterjack toad population that has been studied intensively for more than 20 years (Banks, Beebee & Denton, 1993). Adult natterjacks at this site show a strong preference for open, almost unvegetated terrestrial habitats including sand thinly covered with bryophytes and areas where trees have recently been clearfelled (Denton & Beebee, 1994). A total of fourteen 20 x 20 metre squares of terrestrial habitat were demarcated at the start of the experiment to include: (a) four bryophyte

areas; (b) four areas of grassy clearfell, which were partly vegetated with low-growing grasses; (c) four areas of completely bare sandy clearfell; and (d) two patches of recently-mown callunetum heath, with an average stem height of about 5 cm. Two each of (a)-(c) were within an area grazed from May-September each year by domestic (highland) cattle at a density of approximately one adult animal per three hectares of heathland. There were no mown patches within the grazed areas. The squares were separated from each other by at least 10 metres but were not enclosed, and animals were free to emigrate or immigrate at all times. The habitat types demarcated by squares were intermixed and not separated in clearly defined zones, and no particular habitat type was consistently nearer the breeding ponds than any other. In the first year of the experiment (1992), B. calamita tadpoles were reared to metamorphosis and toadlets grown in captivity, feeding them with hatchling crickets, to an average length of 15 mm. Seventy-five toadlets were released on each experimental square in late summer, and each square was provided with two or three tiles (Denton & Beebee, 1992) as cover to increase initial survival. During the second year of the experiment a further batch of toadlets (averaging 16 mm long) were given individual toe-clip marks and 20 released onto each experimental square in late summer.

Squares were inspected twice monthly during the activity periods of year one (late summer/autumn after first release), year two (April-September) and year three (April-September) and all sightings of toadlets recorded without attempting to identify individuals. Each square was searched for about 15 minutes during each visit, including the inspection of potential refugia, and always on bright sunny days when toadlets were expected to be active (Beebee, 1983). Adult natterjacks and common toads present in the squares were also recorded, as well as animals present on the

TABLE 1. Effects of grazing and habitat type on habitat occupancy. Data are averages for squares where these were paired, with standard deviations in parentheses, and represent total sightings of totalets summed over the study period, and total separate individuals of adult *B. calamita* and *B. bufo*, pooled in all cases over three years

	Bufo co Released	<i>alamita</i> I toadlets	Residen	<i>Bufo bufo</i> Resident adults		
Habitat	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Bryophytes	16.0(14.1)	26.5(16.3)	8.5(7.8)	6.5(3.5)	0(0)	(0)
Grassy clearfell	12.5(9.2)	10.5(4.9)	5.0(7.1)	9.5(10.6)	1.0(1.4)	0.5(0.7)
Bare clearfell	10.5(7.8)	0.5(0.7)	2.5(3.5)	0(0)	1.0(1.4)	0(0)
Mown heath	1.5(2.1)	/	0(0)	/	0(0)	/
Total sightings/nos.	81	75	32	32	4	1

(A)) SURVIVAL AND ABUNDANCE WITHIN EXPERIMENTAL SQUARES
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(B) TOAD DISTRIBUTIONS OUTSIDE EXPERIMENTAL SQUARES

	<i>Bufo ca</i> Released	alamita toadlets	Residen	t adults	Bufo bufo Resident adults	
Habitat	Ungrazed	Grazed	Ungrazed	Grazed	Ungrazed	Grazed
Bryophytes	20.0(2.8)	5.0(1.4)	35.5(0.7)	5.0(0)	0(0)	0(0)
Grassy clearfell	5.5(3.5)	5.5(4.9)	2.5(2.1)	3.0(0)	2.0(2.8)	0(0)
Bare clearfell	5.0(0)	0(0)	4.0(1.4)	0(0)	0(0)	0(0)
Mown heath	0(0)	/	0(0)	/	0(0)	/
Pond basins	14.5(0.7)	6.5(0.7)	2.0(0)	1.0(1.4)	5.0(0)	0(0)
Total	45	17	44	9	7	0

same habitats outside the squares on all parts of the study site. Adults were identified and recorded as individuals rather than total sightings, based on throat spot patterns and other morphological features (Denton & Beebee, 1993). Numbers were log-transformed and subjected to statistical analysis using the MINITAB package on an IBM PC.

RESULTS

Total records for the experimental squares, cumulative over the three years of study, are shown in Table 1A. No attempt was made to distinguish individual toadlets on the replicated squares, and no more than three were seen on any one square during a single visit. Since a total of 95 toadlets was released onto each square during the experiment, mortality or emigration was presumably high though the proportion of toadlets present that were actually observed could not be estimated. In any case, high (>95%) mortality or emigration rates are to be expected at this phase of life (Beebee, 1983; Banks, Beebee & Denton, 1993). Adult toads, on the other hand, could be individually recognised and data for them represent numbers of animals using the squares over the three years. Repeat observations of the same individual were therefore not scored. The entire area occupied by natterjacks at Woolmer was also inspected at regular intervals and toadlets as well as adults quantified in the same way, as shown in

Table 1B. Grazed and ungrazed areas were very different in total extent (6 ha and >30 ha respectively) and thus numbers of animals on them were not comparable in absolute terms.

Two-way analysis of variance indicated no significant differentiation of habitat occupancy between the three major types studied or as a function of grazing regime for either natterjack toadlets or adults within the experimental squares (Table 2). However, use of bare clearfell by all age groups was consistently lower in grazed areas than in ungrazed ones both inside and outside experimental squares. Common toads were rarely encountered in the open habitat types preferred by natterjacks and the small numbers seen precluded formal analysis, but there was a strong indication that this species was disfavoured by the grazing regime. Eleven common toads were recorded in prime natterjack habitat outside the grazing area but only a single one within it.

Toadlet survival in the first winter of the study (1992-3) was apparently higher than that of first-year animals (both natural metamorphs and releases) in later ones, though this was not quantified directly and may have related to climatic variation (see Discussion). Interestingly, there was no evidence of size-related selection for survival during the first winter of this study. Thus in October 1992 the mean size of 20 toadlets sampled from a range of squares was 23.3

TABLE 2. Analysis of variance of grazing and habitat effects in experimental squares. ANOVAs compare abundances in (i) grazed and ungrazed; (ii) bryophyte, grassy and bare clearfell habitats.

(A) NATTERJACK TOADLETS

Source	df	SS	MS	F	Р
Grazing	1	5.13	5.13	1.41	0.27
Habitat	2	19.20	9.60	2.63	0.13
Error	8	29.18	3.65		
Total	11	53.51			

(B) NATTERJACK ADULTS

Source	df	SS	MS	F	Р
Grazing	1	0.02	0.02	0.0	0.96
Habitat	2	49.90	24.95	3.07	0.10
Error	8	65.12	8.14		
Total	11	115.03			

(C) MEAN NUMBERS OF NATTERJACKS IN SELECTED TREATMENTS

Adults	Toadlets
5.3	13.0
5.3	12.5
7.5	21.3
7.3	11.5
1.3	5.5
	Adults 5.3 5.3 7.5 7.3 1.3

mm, with a range of 16-33 mm, whereas another random sample of 12 toadlets in spring 1993 showed no significant difference with a mean of 25.0 mm and a range of 18-33 mm.

There was some evidence that toadlets, although accommodating to the same types of habitat used by adults, did not show exactly the same preferences. Pooling observations on both types of clearfell and comparing total observations on the site outside experimental squares (i.e. those of Table 1B), in the ungrazed area toadlets were found less often in bryophyte habitat and more often in pond basins than expected by chance compared with adults ($\chi^2 = 24.38$, df=2, P<0.001). The same was true within the grazed area ($\chi^2 = 13.20$, df = 2, *P*<0.01), but since the observations did not distinguish individual toadlets (and could therefore include pseudoreplication) this statistical test merits cautious interpretation. Nevertheless, the occupancy of damp pond basins by toadlets in their first year of life persisted long after metamorphosis, and in autumn many were observed making their first burrows in this habitat.

DISCUSSION

Interpretation of the observations described in this paper must be made with caution for several reasons. Firstly, there could be differences between the habitats in toadlet visibility which would bias recording. However, all the habitats studied were open and sparsely vegetated and we do not believe that differential observability was a substantial cause of variation. Sightings of more than one toadlet on a square during a single visit, for example, were not confined to particular habitat types but were apparently random in this respect. Secondly, the animals were free to wander into and out of the squares and we cannot distinguish between mortality and emigration as determinants of observation frequency. However, we were only concerned with whether the habitats were comparable in their suitability for toadlets and sightings should still reflect this whether or not mortality or migration was the dominant influence, or even whether or not it varied between habitat types. Thirdly, for toadlets we scored sightings rather than individuals because we did not find it possible to make identifications with certainty. Although some toadlets were given specific toe-clips in the second year of study, survival of marked animals was extremely low and therefore not very useful to the investigation. This experiment did, however, indicate how mobile young toadlets can be since two marked individuals were found in pond basins several hundred metres from their release points. Fourthly, data on experimental squares could have been confused by immigration of toadlets produced by the natural breeding ponds. We believe that this is unlikely to have made a significant impact, partly because natural levels of metamorphosis were low (almost zero) during the critical first year of the study period and partly because most of the squares were well away from the breeding ponds. The results of the statistical tests must also be considered carefully within the limitations of the methodology employed, and it remains possible that the available statistical power in this situation was insufficient to distinguish real differences that might have been present.

Taking account of the above caveats, we nevertheless draw two tentative conclusions from this study. Firstly, we found no evidence of extra microhabitat requirements specific to toadlets over and above those needed by adults at some time during the year. Inside or outside experimental squares (natural metamorphs presumably predominating in the latter category) we never observed toadlets in habitat types unused by adults, although the occupancy of desiccated but still damp pond basins by young toadlets, sometimes for months after metamorphosis, was notable. Secondly, the low-density livestock grazing regime in place on part of the heath was apparently compatible with natterjack survival and may benefit them by disadvantaging the competitively-superior Bufo bufo (Banks & Beebee, 1987). Grass snakes Natrix natrix, a

major predator of B. calamita at Woolmer, also tended to avoid ponds inside the grazed area presumably because cover around the pond margins was much reduced (unpublished observations) while cattle dung stimulated growth rates of natteriack tadpoles in the oligotrophic heathland ponds (Denton & Beebee, in preparation). Only on bare sand within the grazing area were natteriacks of all ages scarce or absent, but this was almost certainly because the bare sandy clearfell in the grazed zone was subject to heavy winter flooding (and thus not strictly comparable with otherwise similar terrain outside it), a difference not realised until after the experiment was underway. The limited space within the grazing area did not, in any case, allow for selection of alternative bare clearfell areas. We suspect that winter flooding substantially increases mortality of young natterjacks at Woolmer, which was apparently high in all parts of the site during the wet winters of 1993-4 and 1994-5 but much lower under the drier conditions of 1992-3. Cattle trampling, by contrast, was extremely beneficial on grassy clearfell where it broke up turf and facilitated burrowing. More toadlets were found in these sites in year three compared with years one and two, indicating a progressive improvement in habitat quality over several seasons. Grazing regimes should bring many benefits to heathland conservation provided the density of animals is not too high, and at Woolmer the stocking rate of one cow per three hectares dramatically reduced the extent of invasive Molinia grasses as well as impacting upon scrub and pine (Pinus sylvestris) encroachment with minimal damage to areas of mature callunetum.

There is still much to learn about the first years of life of wild amphibians. Methods to address this problem are few and difficult, and at present are less able than comparable work on adults or larvae to produce clear results. The study reported here has generated some extra information on juvenile life that should be useful in planning conservation management for a species currently endangered in Britain and some other parts of northern Europe.

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SHORT NOTES

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ECOLOGICAL NOTES ON AN ISOLATED POPULATION OF THE SNAKE ELAPHE QUATUORLINEATA

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The four-lined snake (*Elaphe quatuorlineata*), an oviparous colubfid up to 2.5 m long, is one of the largest European snake species (Bruno & Maugeri, 1990). Despite its broad European distfibution, the ecology of *Elaphe quatuorlineata* is still poorly known because of its very secretive behaviour (Pozio, 1976; Cattaneo, 1979, and see Böhme & Seerbak, 1993 for a review).

In many areas of its Italian range, the four-lined snake is declining (Corbett, 1989), primarily because of habitat loss due to human activities. This decline seems to be more serous in very industrialized and intensively cultivated areas, such as the neighbourhood of Rome (central Italy), where the species is found in only small and scattered populations (Capula, 1989; Rugiero, unpubl.). The total lack of information on the biology of such scattered *E. quatuorlineata* populations is a major obstacle to the formulation of conservation strategies for preventing this species' further decline.

During a long-term research study on reptile biology in the Roman region conducted by one of us (L. Rugiero), ecological information on a four-lined snake population has been collected. This information may be of some interest either for conservation measures or for augmenting the scarce knowledge of *E. quatuorlineata* biology. Therefore, in this paper we present and discuss the results obtained on such a snake population.

Aft data given here were collected between February 1989 and early November 1994 in a forested area situated near the village of Tor Lupara, about 17 km east of Rome (latitude: 42' N; longitude: 12'40'E of Greenwich; about 70-100 m above sea level), where other studies on reptile ecology were simultaneously conducted (Rugiero, 1993; Rugiero & Luiselli, 1995). The total area surveyed was about 40 ha. The habitat was characterized by a forest (Quercus cerris, Ulmus minor, Carpinus betulus) bordered with herbaceous pastures. The forested zone was completely surrounded by cultivated fields, busy roads and urban areas which are inhospitable to snakes. Thus, the snake population studied here can be considered as virtually isolated. The climate of the area is typically Mediterranean, with mild and rainy winters, and hot and dry summers.

Thirty field trips per year were conducted, each eight hours long. This constant sampling effort was necessary to ensure that the number of snakes recorded per year was a true reflection of the population status and not just a representation of sampling effort.

When a four-lined snake was encountered, it was captured by hand, sexed, measured to total length (to the nearest 0.5 cm) and weighed (to 0.1 g with an electronic balance); scale-clipped and painted on the dorsal surface with a blue number for further visual identification. Moreover, its feeding status was determined by palpation of the abdomen. In order to avoid excessive disturbance to the few specimens in the area, we avoided forcing them to regurgitate their ingested prey, and limited our investigation of food habits to the analysis of faecal pellets collected from live specimens (e.g. Monney, 1990; Luiselli & Rugiero, 1993). The density of some prey types (lizards and small mammals) at the study site was estimated as a part of the field work (see Rugiero & Luiselli, 1995 for both methods and results). The clutch size of some (n = 6) gravid females was estimated by palpation of the abdomen, a method very useful and very accurate in the field (Bonnet & Naulleau, 1994). Two of these females were transferred to the laboratory, where they layed eggs. The eggs were incubated on vermiculite at ambient temperature, and all the offspring were permanently scale-clipped and then released in the field. The statistical analyses were done by Statgraphic 2.0 computer package, with α assessed at 5%.

Population size. The four-lined snake is very rare in the area, while sympatric Coluber viridiflavus, Elaphe longissima, Natrix natrix and Vipera aspis are more common. In fact, while the populations of all these other snakes consisted in each year of at least thirty adults, the highest number of different *E. quatuorlineata* specimens (including both adults and juveniles) captured during one year of research was 16 (in 1989, see Table 1). However, since 1990 this number decreased and then remained stable at around 10 (Table 1). The recaptures were frequent between years. The sex-ratio was apparently skewed in favour of the males in every study year, but the difference was never significant (binomial test, in all cases P>0.1).

Food habits. A ltogether, we obtained remains of 30 prey items from a total of 24 faecal pellets, most of

TABLE 1. Total number of snakes captured in each year. Juveniles and adults are pooled together, but sexes are counted separately.

Year No. males No. females Total Apparent sex-ratio	_
1989 10 6 16 1.67:1	
1990 5 3 8 1.67:1	
1991 6 4 10 1.50:1	
1992 6 4 10 1.50:1	
1993 7 4 11 1.75:1	
1994 7 5 10 2.33:1	

TABLE 2. Prey composition of *Elaphe quatuorlineata* at the study area

Prey type	Ν	%N
Podarcis muralis	7	23.3
Passeriformes (indeterminate)	5	16.7
Apodemus sp.	12	40.0
Rattus sp.	3	10.0
Muridae (indeterminate)	3	10.0
TOTAL	30	100.0

which came from endothermic vertebrates (Table 2). The small amount of data collected prevented us making comparisons of diet composition between sexes or between seasons. Lizard remains were found in faeces obtained only from immature indmduals: the largest snake that preyed on a lizard was a male 89.4 cm long. Conversely, the diet of the adults was composed only of birds and rodents, as previously observed by Cattaneo (1979) in another area of the Roman countryside. Contingency-table analysis revealed that the ontogenetic shift in dietary composition (from ectotherm to endotherm prey) is statistically significant (χ^2 , P<0.005, see Fig. 1). A similar dietary shift is present in other Mediterranean populations of snakes studied previously (e.g. Saint Girons, 1980; Luiselli & Agrimi, 1991). Comparing the dietary data of E. quatuorlineata with those of sympatric C. viridiflavus (see Table 1 in Rugiero & Luiselli, 1995), it should be noted that the food preferences of the juveniles of both species are very similar (χ^2 , P>0.1), while the food preferences of the adults differ considerably (χ^2 , P<0.005) because of either the high frequency of utilization of the lizard resource by adults Coluber or of the high frequency of utiliztion of the bird resource by adult Elaphe. Podarcis muralis and Apodemus sylvatica, respectively the most available lizard and rodent species in the area (Rugiero & Luiselli, 1995), were also the most common prey types in both E. quatuorlineata and C. viridiflavus. This occurrence suggests that both these colubrids are opportunistic predators (see also Capizzi et al., 1995; Rugiero & Luiselli, 1995).



FIG. 1. Ontogenetic change in the diet of *Elaphe quatuorlineata* from Tor Lupara, Rome (central Italy). Black bars represent endothermic prey (small mammals and birds), while white bars represent ectothermic prey.

Growth. Growth was estimated in seven different specimens (five males and two females) of known age and recaptured throughout the years. Table 3 summarizes the size of these specimens at different ages. Maturation was estimated at a minimum age of over 3 years in the males and over 3.5 years in the females, although the gravid females in our sample were always older (at least five years of age). In fact, the males longer than 90 cm were found to participate in the spring sexual activity, while the smallest mature female was 117 cm long (although the smallest gravid female captured by us was 132 cm long).

Fecundity. Clutch size of six adult females was estimated. There was a significant positive relationship between female size (TL, in cm) and clutch size (Pearson's r=0.85, $r^2=73\%$, $F_{1,4}=10.8$, P=0.03). This positive relationship is a widespread occurrence in snakes (e.g. see Saint Girons & Naulleau, 1981), espe-

TABLE 3. Size of males and females *Elaphe quatuorlineata* at different ages. Only specimens of known age are considered. Five specimens that were of unknown age at the moment of first capture are excluded from this table.

	Total length (cm) of each individual at different ages									
Year	0	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5
Individual:										
male 1	37.4	39.5	42.3			89.4		97.6		
male 2	33.6				61.1					
male 3	35.8	44.2				82.6	93.1			
male 4	36.7		59.7							
male 5	37.6				70.0			117.0	119.0	122.2
female 1	33.8			63.2	68.7					
female 2	34.7			63.6	81.4		102.5			

cially in those places where food is not a limited resource (Andrén & Nilson 1983; Capula & Luiselli, 1994; Luiselli et al., 1996). The mean number of eggs produced by a female was 10.83±1.17, while the pregnant females averaged 155.16±11.65 cm. In another Mediterranean area of central Italy (Tolfa mountains, province of Rome), where E. quatuorlineata is widespread and relatively common, the females copulate for the first time three years of age, and the mean length of the gravid females is about 125 cm TL (E. Filippi, unpublished data). Thus, compared with the small population studied here, the female E. quatuorlineata of Tolfa show (1) a slightly earlier maturation and (2) a lower mean body size when pregnant. Though more detailed comparisons are necessary before stressing firm conclusions, we suggest that these differences between our isolated population and these other populations living in more suitable areas indicate a declining status in the former population. According to Stearns (1976), in fact age at maturity may be a lifehistory trait acted on by natural selection and is dependent on the demographic environment of the various populations: individuals in growing populations may tend toward earlier maturity and individuals of declining populations may mature later. The small size of this isolated population is arguably another evidence of its declining status.

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CORRELATES OF APPROACH DISTANCE IN THE STRIPED PLATEAU LIZARD (SCELOPORUS VIRGATUS)

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Animals often exhibit state-dependent behaviour, i.e. behaviour that depends on their present situation or state. In lizards, escape behaviour appears to be statedependent and several factors affect it. Tail loss influenced escape behaviour in Scincella lateralis. Lizards without tails permitted a model predator to approach closer than lizards with tails (Formanowicz, Brodie, & Bradley, 1990). Snell, Jennings, Snell, & Harcourt (1988) found that Tropidurus albemarlensis in vegetatively complex habitats were less wary (i.e., had shorter approach and flight distances) than individuals in less complex habitats, presumably because of reduced exposure to predators. Bulova (1994) obtained similar results when comparing populations of Callisaurus draconoides. Similarly, Martín and López (1995a, b) found that approach distances and flight distances of Psammodromus algirus were shorter in more open habitats and microhabitats.

Body temperature can also influence lizard escape behaviour. Anolis lineatopus flee at greater distances when they are cool and allow a predator to approach closer when they are warm (Rand, 1964). Other lizards flee farther or to different microhabitats at different temperatures (Losos, 1988). Several species of lizards become more aggressive at lower body temperatures, and will attempt to flee at higher body temperatures (Hertz, Huey, & Nevo, 1982; Crowley & Pietruszka, 1983; Mautz, Daniels, & Bennett, 1992). Escape behaviour in gravid females involves crypsis (as opposed to more active behavior in non-gravid females) in Eulamprus tympanum (Schwarzkopf & Shine, 1992), Lacerta vivipara (Bauwens & Thoen, 1981), Podarcis muralis (Braña, 1993) and Callisaurus draconoides (Bulova, 1994). Lizards can also learn to avoid predators, and have been shown to flee more quickly after just one capture (Marcellini & Jenssen, 1991). Other important factors influencing lizard escape behaviour include distance to cover (Bulova, 1994), the approach behaviour of the predator (e.g., direct or tangential; Burger & Gochfeld, 1990; Burger, Gochfeld & Murray, 1991; Bulova, 1994), the physical appearance of the predator (e.g., eye size, Burger, Gochfeld & Murray, 1991; exposed face, Burger & Gochfeld, 1993), the age or size of the lizard (Martín & López, 1995b) and the presence of efficient predators (e.g., cats; Stone, Snell, & Snell, 1994). In this study, I examined the escape behaviour of the striped plateau lizard, *Sceloporus virgatus* Smith, from a population in the Chiricahua Mountains of southeastern Arizona.

Sceloporus virgatus is a common terrestrial lizard in the pine-oak woodlands of the Chiricahua Mountains. It is most often found on rock and log substrates (Smith, 1995). The study area was located in the Coronado National Forest, 2.5 km SW of the Southwestern Research Station in the Chiricahua Mountains of southeastern Arizona. The area consisted of a 1.2 km section of pine-oak woodland in a creekbed with north and south facing slopes. Two types of habitat were identified along the study site: (1) a woods habitat consisting primarily of rocks and trees, and (2) a slide habitat consisting primarily of slopes covered with bare rock or gravel with sparse grass clumps and occasional trees and larger rocks. Common predators observed on the study site include birds (Mexican Jays) and snakes (black-tailed rattlesnakes, mountain king snakes, and bullsnakes). This study took place during the third year of an intensive mark-recapture study on this population (Smith, 1995).

I measured approach distance by slowly and directly approaching a stationary and undisturbed lizard at a constant speed and estimating the distance at which the lizard first fled from my approach (to nearest 0.1 m). In addition to approach distance, I recorded the substrate (rock or log), habitat (woods or slide), and slope (north- or south-facing) the individual was initially observed on or in. Body size (SVL) from the most recent capture was used in analyses. Mark-recapture studies allowed me to assess reproductive condition of females (i.e., gravid or non-gravid), and to assess whether the individual's tail had ever been broken (i.e., freshly broken or regenerated tails), as well as to record the number of days since the last capture and how many times an individual had been previously captured in the current season. Assumptions of parametric analyses (normality and homogeneity of variances) were not violated, and therefore parametric analyses were used. Means are given \pm one standard error.

A total of 71 independent observations was made (i.e., one measurement per individual). In most cases, individuals ran to the nearest cover (e.g., under a rock). Also, it appeared that the approached lizards were aware of my presence well before flight because their heads were often turned towards me as I approached.

Substrate ($F_{1,68} = 1.66$, P = 0.20), habitat ($F_{1,70} = 0.21$, P = 0.64), and slope ($F_{1,70} = 0.04$, P = 0.84) had no significant effects on flight distance (see Table 1 for means). Sex ($F_{1,69} < 0.001$, P = 0.99) and reproductive

	Ν	Approach distance (m)
Substrate		
Rock	41	2.1 <u>+</u> 0.2
Log	28	1.8 <u>+</u> 0.2
Habitat		
Woods	55	2.0 ± 0.2
Slide	17	1.9 ± 0.2
Slope		
North-facing	43	2.0 ± 0.1
South-facing	29	1.9 <u>+</u> 0.2
Sex		
Male	38	2.0 <u>+</u> 0.2
Female	33	2.0 <u>+</u> 0.2
Reproductive State		
Gravid	21	1.9 <u>+</u> 0.2
Non-gravid	12	2.2 <u>+</u> 0.3
Tail Condition		
Broken	21	1.4 ± 0.2
Whole	50	2.2 <u>+</u> 0.2

TABLE 1. Mean $(\pm 1 \text{ SE})$ approach distance for *Sceloporus* virgatus in the Chiricahua Mountains of southeastern Arizona by substrate, habitat, slope, sex, reproductive state (females only), and tail condition.

state ($F_{1,31} = 0.53$, P = 0.47) also had no significant effect (see Table 1 for means). Approach distance was not related to SVL (linear regression: N = 71, $r^2 = 0.001$, P = 0.84), and number of days since last capture (N = 65, $r^2 = 0.014$, P = 0.35). However, approach distance was negatively related to the number of previous captures in 1994 (N = 71, $r^2 = 0.14$, P = 0.002; y = 2.7 - 0.46x), but little of the variation (14%) in approach distance was explained. Individuals that had broken tails allowed me to approach closer than individuals that did not have broken tails (Table 1; $F_{1.69} = 11.26$, P = 0.001).

This study suggests that striped plateau lizards alter their escape behaviour as a function of their current state (i.e., whether the individual has broken its tail in the past or not). In cases where female sprint speed is decreased by being gravid, females often rely more on cryptic behaviour than flight responses (Bauwens & Thoen, 1981; Schwarzkopf & Shine, 1992). Tail loss can decrease sprint speed in lizards (Ballinger, Nietfeldt, & Krupa, 1979; Punzo, 1982; Dial & Fitzpatrick, 1984), thus if tail loss decreases sprint speed in *S. virgatus*, individuals with tail breaks may assume a more cryptic behavior and allow predators to approach closer before fleeing. Indeed, Formanowicz *et al.* (1990) have experimentally demonstrated this scenario in the ground skink, *Scincella lateralis*. In addition, tail loss can lead to different patterns of microhabitat use which compensate for reduced speed by decreasing the distance to refuges (Martín & Salvador, 1993). I predict then that a shift to a more cryptic anti-predator strategy among lizards that have lost their tails will be a common strategy in terrestrial lizards, such as many sceloporines and skinks. The role of tail loss in the escape behaviour of arboreal lizards is largely unknown at this time. However, in species that use their tail for balance (e.g., *Anolis carolinensis*; Ballinger, 1973), a cryptic anti-predator strategy will probably also occur.

One alternative explanation might be that individuals that allow predators to approach more closely are more likely to lose their tails, thus the relationship between tail loss and antipredator behaviour is reversed from the scenario discussed above (Burger & Gochfeld, 1990). Another alternative explanation is that individuals learn from previous encounters with predators (assuming tail loss associated with predation), and use a different escape strategy after encountering a predator. This explanation is supported by the decrease in approach distance with an increase in the number of previous captures for an individual. To differentiate between these alternative hypotheses experiments involving manipulation of tail loss, and on the effect of tail loss on sprint speed in *S. virgatus* are needed.

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ADVERTISEMENT CALLS OF TWO BOLIVIAN TOADS (ANURA: BUFONIDAE: *BUFO*)

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Bufo poeppigii is a species of the Bufo marinus group occurring on Amazonian slopes of the Andes from Colombia to Bolivia (Frost, 1985). The taxonomic status of this toad has been in state of flux since its description, but it is now clear that it is a valid species (De la Riva, Marquez & Bosch, 1995). On the other hand, populations usually recognized as Bufo "typhonius", occurring from Panama and the Chocoan region of South America to southeastern Brazil, throughout the entire Amazon basin and Guianas, represent a complex of species and its proper name is Bufo margaritifera complex (Hoogmoed, 1986, 1989, 1990; Hass, Dunsky, Maxson & Hoogmoed, 1995). Bolivia is one of the regions where the systematics of this complex is obscure. Data on recordings of the advertisement calls may be a useful tool in order to distinguish between the different forms presumably involved. Discussions on the taxonomic status of both B. poeppigii and the B. margaritifera complex in Bolivia are beyond the scope of this study, except in the the context of the differences in the advertisement calls. Thus, the goals of this paper are: (1) to describe for the first time the advertisement call of B. poeppigii, and compare it with that of its close relative, B. marinus; and (2) to provide data on the advertisement calls of two different populations of the B. margaritifera complex from Bolivia, and compare them with recordings obtained by other authors from populations of the same complex elsewhere.

Recordings were obtained in 1990 and 1994. Materials and methods used in recording and analysing data are explained in other papers by us [see for example Marquez, De la Riva & Bosch (1993)]. Voucher specimens 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.

Recordings of *Bufo poeppigii* were obtained at Bulo-Bulo, Province Carrasco, Department of Santa Cruz, Bolivia (17° 16' S; 64° 20' W), where males called at night from ephemeral rain-filled puddles, in a

disturbed area near human settlements. Some specimens were calling from the shore of the puddles, whereas others were in the water with the body partially submerged. Air temperature was 25.4°C at the time of recording. The call (Fig. 1) was loud and emitted at regular intervals (mean call rate, 16.3 calls per min.). The call was a train of 10-45 pulse groups (sensu Schneider & Sinsch, 1991) emitted at a regular rate (17.0 pulse groups per second), forming a call with variable duration (631.0-2680.6 ms). Most calls were formed by a long train of pulse groups but some showed an interruption and two shorter pulse trains were emitted in quick succession. Each pulse group was composed of 3-5 pulses emitted at regular intervals (mean pulse rate within pulse group, 131.7 pulses/s). The dominant frequency of the calls was 1033.2 Hz, although power was present in 750-1500 Hz range.

No previous recordings of *B. poeppigii* are available for comparison. A related species, which is sympatric with *B. poeppigii* at Bulo-Bulo, is *B. marinus*. Calls of *B. marinus* were analysed by Schlüter (1981, 1984) in Panguana, Peru. Because *B. poeppigii* could also occur in Panguana, and this is a species of which the taxo-



FIG. 1. Audiospectrogram and oscillogram of a 2.5 s section of a characteristic advertisement call of *Bufo poeppigii* recorded at Bulo-Bulo, Bolivia.



FIG. 2. Audiospectrogram and oscillogram of a 2.5 s section of a characteristic advertisement call of *Bufo margaritifera* recorded at La Bola, Bolivia.

nomic status has been subject of controversy, we have to be cautious when considering the population of toads from Panguana. However, the species in this locality has always been considered to be B. marinus by the different authors working in the area (Toft & Duellman, 1979; Schlüter, 1981, 1984; Aichinger, 1987; 1991). In fact, the available data on calls of toads from Panguana seem to indicate that B. marinus is the species occurring there (or, at least, the recorded species). Schlüter (1981; 1984) found a range frequency between 300-1000 Hz, and his Fig. 1 (Schlüter, 1981: p.100) shows a call consisting of 20 pulses at an interval of about 1400 ms. These data indicate a lower pitched call than that of B. poeppigii. Easteal (1986) shows an audiospectrogram of the call of B. marinus from Tinalandia (western Ecuador), with a duration of about 2000 ms, containing more than 20 pulses, and with the highest frequency hardly reaching 1000 Hz. Again, this is a lower frequency call than that of B. poeppigii. One of us (DLR) heard B. marinus calling at Valle de Sajta, a locality near Bulo-Bulo. The call was structurally similar to that of B. poeppigii, but also sounded lower in frequency. This difference may be simply due to the larger size of B. marinus in comparison to *B. poeppigii*. As was pointed out by Blair (1964) [see also Martin (1972)], in the genus Bufo, unless atypical allometric growth of the larynx is present, the smaller the animal, the higher the dominant frequency. Thus, given that the calls of B. marinus and B. poeppigii differ mainly in the dominant frequency, this difference might be explained solely by the difference in size between both species.

Recordings of toads of the B. margaritifera complex were obtained at La Bola, Department of Santa Cruz (17° 48' S; 62° 50' W), a Chacoan area near the city of Santa Cruz de la Sierra, and at Puerto Almacén, northwestern Department of Santa Cruz (15° 46' S; 62° 15' W), an Amazonian locality in wet subtropical forest (Tosi et al., 1975). At La Bola, where air temperature was 23.5°C at the time of recording (a single observation), a few males called at night in ephemeral ponds, whereas in Puerto Almacén, although males sometimes formed choruses and called around ephemeral ponds, most of the observations were made on males calling from stream banks (De la Riva, 1993). Normally, the calling site is right on the shore, although sometimes the individuals were partially submerged. The call (Fig. 2) was loud and emitted at regular intervals (mean call rate, 57.0 calls/min). It consisted of a train of 5-7 pulse groups (sensu Schneider & Sinsch, 1991) emitted at regular intervals (26.6 pulse groups/ s), forming a call with variable duration (197.3-291.6 ms). Each pulse group was composed of 1-4 pulses emitted at regular intervals (mean pulse rate within pulse group, 102.1 pulses/s). The mean dominant frequency was 1332.3 Hz, and energy was distributed in the 500-1500 Hz range. Calls from La Bola and Puerto Almacén were almost identical, and the toads themTABLE 1. Summary of the numerical parameters (mean±SD, range) of the vocalizations of *B. poeppigii* and *B. margaritifera*

	B. poeppigii	B. margaritifera
Individuals analysed	1	3
Calls analysed	19	32
Call duration (ms)	1760.4±598.7 631.0-2680.6	238.2±22.9 197.3-291.6
Dominant freq. (Hz)	1033.2±71.6 907.0-1141.3	1332.3±107.0 1211.5-1544.7
Pulse groups/call	29.9±10.1 10.0-45.0	6.3±0.6 5.0-7.0
Pulses/pulse group	3.3±0.6 3.0-5.0	2.0±0.5 1.0-4.0
Pulse groups/second	17.0±0.6 15.8-17.8	26.6±2.1 22.4-30.1
Pulses/second	131.7±13.2 99.0-146.0	102.1±17.4 52.2-149.2
Pulse duration/period	0.4±0.1 0.3-0.6	0.5±0.1 0.2-0.9
Calls/min.	16.3±8.9 5.6-37.3	57.0±18.6 31.3-95.2

selves looked similar. In Table 1 are the pooled data from both localities. A slightly higher frequency was detected in the Puerto Almacén recordings, which may be due to a smaller size of the calling male. Thus, it seems that Chacoan populations do not differ from Amazonian Bolivian ones. Although members of the *B. margaritifera* complex have been always considered as rainforest species that can enter cloud forest up to 1840 m (Duellman, 1978), in Bolivia they also occur in the temperate Andean valleys to 1400 m (De la Riva, pers. obs.), and extends over the northern Chaco at least to the latitude 19° 27' S (De la Riva, 1990; De la Riva, Castroviejo & Cabot, 1992).

The calls of some populations of toads in the *B.* margaritifera complex have been described and analysed by Duellman (1978) and Schlüter (1981) (as *B. typhonius*), in Santa Cecilia (Ecuador) and Panguana (Peru), respectively. Duellman (1978) found a call of only 3-5 rapid notes (= pulses), lasting 150-200 ms, with a dominant frequency of about 1500 Hz. Thus, these Ecuadorian toads seem to emit a call that is slightly shorter and higher pitched than are the calls of the Bolivian toads On the other hand, the results presented by Schlüter (1981) show a call with a broader range of frequencies (800-2200 Hz) and a higher number of pulses, as may be observed in his Fig. 4

(Schlüter, 1981: p.103). Although some caution is needed given the small samples considered, the differences observed between these results and ours could be indicative of species-level differences. This would be not unexpected, given the presumably small areas of distribution of some of the species in the complex, and the apparent concentration of species in the Amazonian regions of Ecuador and northern Peru (Hoogmoed, 1990).

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CALL CHARACTERISTICS AND SYSTEMATIC RELATIONSHIPS OF A MALAYAN TREEFROG NYCTIXALUS PICTUS (ANURA, RHACOPHORIDAE)

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Nyctixalus Boulenger, 1882 is a small genus among the Old World tree frog family Rhacophoridae, and includes only three or four species that are confined to Southeast Asia (Frost, 1985). The genus has been variously treated taxonomically as Hazelia (Taylor, 1920; Liem, 1970), Philautus (Inger, 1966), or Edwardtayloria (Marx, 1975). The genus is unique both in morphology and in breeding habit (Inger, 1966; Liem, 1970), and its systematic position among rhacophorids was once assessed chiefly on the basis of morphological evidence (Liem, 1970). Acoustic characteristics of species of the family Rhacophoridae have been rather well-studied among Asian anurans (e.g., Kuramoto, 1986; Matsui & Wu, 1994), but species of Nyctixalus have never been acoustically studied until now (Inger & Stuebing, 1989). In this short note, I will report the call characteristics of N. pictus from Sarawak, Borneo, which is the type locality of the species, and discuss the systematic relationships of this genus to other Asian rhacophorid genera.

Calls of three males of *N. pictus* were recorded at the Park Headquarters, Mulu National Park, Miri Division, Sarawak, Malaysia on 28 and 29 July 1993. Possible advertisement calls (see below) were recorded in the field with a cassette tape recorder (Sony TC-D5) with an external microphone (Sony ECM-23F) and analyzed using computer programs, SoundEdit Vers. 2 or SoundEdit Pro (MacroMind-Paracomp, Inc.) by a Macintosh computer. Air temperatures recorded near the calling males were 23.6-23.7°C.

In the following description, note interval means the time from the end of one note to the beginning of the next note. For statistic analyses, Dunn's multiple comparison test (Zar, 1984) was utilized. The significance level was set at P=0.05.

Males were found calling from low vegetation (< 1 m) at night in the forest. The places where they were calling were not near any obvious breeding sites. Calls were soft and weak, being very similar to those of insects (Fig. 1) and included six to 11 notes (Table 1), each of which was clearly divided into three types (A-C).

The type A note is a long "*fiii*". The note (Fig. 1) was unpulsed and the length varied from 224 to 368 ms with the mean (\pm SD) of 284.7 \pm 40.9 ms (*n*=15). The note was very clearly modulated in frequency (Fig. 1), beginning from 2650 to 2800 hz (mean

 \pm SD=2716.0 \pm 47.6, *n*=15) and ended at 3020 to 3700 hz (mean \pm SD=3281.3 \pm 180.9, *n*=15) (Fig. 1). The dominant frequency measured at the middle of the note varied from 2845 to 3240 hz (mean \pm SD=2998.7 \pm 93.7, *n*=15). Due to heavy background noise of mainly insect calls, it was difficult to analyze frog calls at frequency ranges of 4000 to 8000 hz (Fig. 1), but harmonics were detected at about 8000-10000 hz, although they were very weak and only partial. The type A note was usually emitted singularly, but when the type B notes followed it, the interval between them ranged from 161 to 931 ms (mean \pm SD=577.0 \pm 338.8, *n*=5).

The type B note was also unpulsed, but a shorter "pi". The note length varied from 46 to 161 ms (mean \pm SD=114.7 \pm 28.8, n=54). The note lacked harmonics and a frequency modulation. The dominant frequency varied from 3025 to 3100 hz (mean \pm SD=3069.3 \pm 20.7, *n*=54). The type B note was seldom emitted singularly; it was sometimes uttered following the type A note, and was often followed by the type C note (Fig. 1). The interval between successive notes varied from 115 to 426 ms (mean \pm SD=209.2 \pm 29.7, *n*=52). The note repetition rate varied from 3.17 to 3.82 per second (mean ±SD=3.54±0.21, *n*=10).

The type C note was again unpulsed, and even shorter than the type B. The note length varied from 23 to 104 ms with the mean of 49.4 ± 25.1 ms (n=19). The note lacked harmonics but usually had a marked frequency modulation (Fig. 1). The frequency began from 2900 to 3150 hz (mean \pm SD=2967.3 \pm 66.7, n=19) but increased rapidly and ended at 3150 to 3400 hz (mean \pm SD=3276.3 \pm 67.4, n=19) (Fig. 1). The range of the dominant frequency at the middle of the note was from 3025 to 3275 hz (mean \pm SD=3121.8 \pm 52.9, n=19).

The type C note always followed the type B. Usually several type C notes were emitted successively, and the interval between successive notes varied from 92 to 249 ms (mean \pm SD=147.9 \pm 50.3, *n*=10). Thus the note repetition rate varied from 4.82 to 9.49 per second (mean \pm SD=7.01 \pm 2.04, *n*=4). The type C note was similar for the human ear to the end notes of the syntopic *Rhacophorus appendiculatus*, but was rather softer.



FIG. 1. A sonagram of *Nyctixalus pictus* call including successive notes of one type A, four type B, and one type C recorded at 23.6° C.

Thus the complete call was composed, in order, of the note types A, B, and C, but the combination of only B and C types was more often heard. The type B notes predominated in number within a call in most cases. The total duration of a call varied from 862 ms in the call with three notes to 3571 ms in the call with eight notes (Table 1).

When pairs of notes were compared, lengths of type A notes were always longer than those of type B, which in turn were longer in duration than type C (Dunn's multiple comparison test: P<0.05). The interval between the type A and the subsequent type B notes, however, was not different from the note interval in the type B, though both intervals were significantly longer than in the type C. The frequency measured at the initial point was not different between types B and C, both of which were significantly higher than type A note. By contrast, the frequency measured at the final point did not differ between the types A and C, both of which were significantly higher than type B notes. Finally, the dominant frequency measured at the middle portion of the note differed significantly among the three types, type C being the highest and type A the lowest.

During observations in the field, no mating, courtship, or male-male fighting was seen in *Nyctixalus pictus*. However, calls of one male were found to elicit another's calls. Therefore, the calling activity surely involves at least the male-male relationship and the recorded calls are assigned to the advertisement call category (Duellman & Trueb, 1986).

In a study of Thaispecies of Rhacophoridae, Heyer (1971) assumed that the call prototype for this family would consist of a component with a wide frequency range, lacking harmonics. He did not actually mention,

TABLE 1.	Variation	in the	e number	of note	elements	and
total durat	ion of calls	in Ny	ctixalus p	oictus.		

Nc	No. note types		es	Call length (ms)	
A	В	С	Total	Mean Range	n
0	3	0	3	862	1
0	4	0	4	1276 (1196-1357)	2
0	4	2	6	1564 (1495-1691)	3
0	4	4	8	1875	1
0	5	1	6	1748 (1564-1932)	2
0	5	2	7	1936 (1587-2116)	6
0	5	3	8	2421 (2243-2599)	2
0	7	2	9	2312	1
0	7	3	10	2455 (2300-2611)	2
0	8	3	11	2864	1
1	4	1	6	1657	1
1	5	1	7	2536 (2381-2691)	2
1	5	3	9	2576	1
1	6	2	9	2645	1
1	7	0	8	3571	1

however, the degree of primitiveness for the six species of four genera he studied.

Later, Kuramoto (1986) suggested a possible course of acoustic divergence in the rhacophorids from Taiwan and Japan. He indicated that the single-pulsed note as seen in *Polypedates megacephalus* (as *leucomystax*) was the most primitive and the multipulsed note with harmonic bands as seen in *Rhacophorus moltrechti* or *R. owstoni* the most advanced. In order to examine the validity of these hypotheses, however, further accumulation of acoustic data for many more rhacophorid species is required.

Kuramoto (1986) at the same time noted that long pulses had not been reported in Rhacophoridae. The notes of *Nyctixalus pictus* are here expressed as "unpulsed", but they, especially in the type A, are indeed regarded as long pulses as defined by Kuramoto (1986). In this respect, the call of this species does not resemble calls of any other rhacophorid species hitherto studied (Heyer, 1971; Dring, 1987; Matsui *et al.* in preparation).

From the phenetic analyses of morphology, Liem (1970) proposed that Nyctixalus (as Hazelia) is related to Chirixalus and Theloderma. Channing (1989) reanalyzed Liem's (1970) data cladistically and concluded that Nyctixalus has a sister relationship with Theloderma but not with Chirixalus. Calls of Chirixalus species (Heyer, 1971; Matsui, unpub. data) are judged to be quite different from those of Nyctixalus. Acoustic traits of Theloderma, on the contrary, have never been reported, and are required for comparisons with Nyctixalus.

On the other hand, the unique calls of *N. pictus*, with unpulsed notes may be related to the habit of breeding in tree holes. Two microhylid species of the genus *Metaphrynella* also breed in tree holes and have unique calls with an unpulsed note (Matsui *et al.*, in preparation).

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BOOK REVIEW

Lizards of Australia and New Zealand. John E. Gray and Albert Gunther (1845-1875). Introduction by Glenn M. Shea. (1995). 80 pp, 20 plates. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA. (Facsimile Reprints in Herpetology. Kraig Adler, Editor.) \$20.00 (cloth).

The most recent in a series of nearly 60 reprints of classic and important books and papers, this modestlypriced volume from SSAR is published in cooperation with the Australasian Affiliation of Herpetological Societies. It comprises two different titles. Firstly, the relevant parts of "The Zoology of the Voyage of H.M.S. Erebus and Terror, under the command of Captain Sir James Clark Ross, R.N., F.R.S., during the years 1839 to 1843" (Gray's "Reptiles" chapter, with eight pages of text and 10 plates, issued in 1845; and Gunther's section of 11 text pages and 10 plates, from 1875). Secondly, Gray's 1867 book on "The Lizards of Australia and New Zealand in the Collection of the British Museum", contributing a further six text pages. (As originally published, it also re-used 18 of the 20 aforementioned plates). The six pages of Shea's introduction provide a background to nineteenth century Australasian herpetology, exploration and collections, with biographical details for Gray and an account of the voyage of Erebus and Terror.

In his first section, Gray describes some 36 lizards (including two from New Zealand), with 129 species (10 from New Zealand) listed in his second. Gunther lists 152 (15 from New Zealand), plus two crocodilians (both Australian) and a rhynchocephalian (New Zealand). Whilst there is certainly some interest in the text, it is the plates, taken from the original lithographs, that are the real glory of the book. The artist, George Henry Ford, satisfied the demands of taxonomic functionality placed upon him by Gray (who scorned figures that were "good for artistic effect [yet] destitute of scientific detail"), while contriving to produce life-like illustrations of animals long-dead by the time that he viewed them at the British Museum. Fifty-two lizard species are featured, along with a tuatara.

Leigh Gillett British Herpetological Society

PUBLICATIONS RECEIVED

Radiation Hazards to Fish, Wildlife, and Invertebrates: A Synoptic Review. Ronald Eisler. (1994). 124 pp. Biological Report 26; Contaminant Hazard Reviews Report 29. US Department of the Interior National Biological Survey, Washington DC (paper).

Sodium Monofluoroacetate (1080) Hazards to Fish, Wildlife and Invertebrates: A Synoptic Review. Ronald Eisler. (1995). 47 pp. Biological Report 27; Contaminant Hazard Reviews Report 30. US Department of the Interior National Biological Survey, Washington DC (paper).

Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation. Reed, F. Noss, LaRoe, Edward T. and Scott, J. Michael. (1995). Biological Report 28. US Department of the Interior National Biological Survey, Washington DC (paper).

Turtles of the United States and Canada. Carl H. Ernst, Roger W. Barbour and Jeffrey E. Lovich. (1994). Smithsonian Institution Press. Washington and London. (cloth).

Snakes of the World. A Checklist Vol. II. Boas, Pythons, Shield-tails and Worm-snakes. K. R. G. Welch. (1994). KCM Books, Taunton, Somerset. £12.50 (paper).

Snakes of the United States and Canada: Keeping Them Healthy in Captivity. Vol. 2: Western Area. John V. Rossi and R. Rossi. (1995). 342 pp.Krieger Publishing Co., Florida. US\$69.50 (cloth).

The Herpetological Publications of Wilhelm Peters. Aaron M. Bauer, R. Günther and Meghan Klipfel. (1995). 725 pp. SSAR, Oxford, Ohio. US\$75.00 (cloth).

Evaluation of a Standard Method for Surveying Common Frogs (Rana temporaria) and Newts (Triturus cristatus, T. helveticus and T. vulgaris). R. A. Griffiths, S. J. Raper, and L. D. Brady. (1996). 29 pp. JNCC Report No. 259. Joint Nature Conservation Committee, Peterborough (paper).

EDITOR'S NOTE

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R. Andrews, P. Arntzen, A. Bauer, D. Bauwens, T. Beebee, D. Blackburn, W. Böhme, K. Boomsma, F. Braña, W. Branch, J. Burger, S. Bush, A. Castilla, K. Christian, C. Ciofi, J. Cooper, D. Crews, C. Cummins, I. Darevsky, J. Davenport, J. Diaz, J. Elliott, S. Evans, A. Flemming, J. Foster, R. Freedman, F. Frye, A. Gardner, S. Gates, A. Gent, C. Gerdhardt, P. Gregory, L. Guillette, A. Hailey, G. Hays, K. Henle, M. Henzl, J. Herron, W. Heyer, J. Holomuzki, M. Hoogmoed, C. Hosie, R. Inger, E. Jacobson, J. Jeffers, G. Johnston, M. Littlejohn, J. Loman, J. Martin, R. Meek, A. Milner, G. Nilson, R. Nussbaum, R. Oldham, A. Rand, C. Reading, Z. Rocek, A. Sainsbury, J. Savage, H. Schneider, H. Strijbosch, R. Shine, U. Sinsch, A. Smart, J. Stamps, B. Sullivan, P. Verrell, L. Vitt, M. Wake, B. Waldman, S. Walls, G. Webb, K. Wells, W. Wüster, J. van Wyk, P. Zwart.

NEW HERPETOLOGICAL SOCIETY IN SLOVENIA

The Societas Herpetologica Slovenia was founded in February 1996, with Marko Aljancic as President and Katja Poboljsaj as Secretary. The aims of this new society are to start a mapping scheme for Slovenian herpetofauna, popularise herpetology (particularly among young people), and to publish an occasional newsletter, *Temporaria*. All herpetologists are invited to become members. Details from: Societas Herpetologica Slovenia, Slovenian Museum of Natural History, Presernova 20, P.O. Box 290, SLO-61000 Ljubljana, Slovenia.



HERPETOZOA is a journal devoted to all aspects of herpetology published by the Austrian Society for Herpetology (Österreichische Gesellschaft für Herpetologie - ÖGH).
ÖGH membership includes the price of subscription to HERPETOZOA (192 pages p. a.).
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HERPETOZOA is cited in the Zoological Record.
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Address to be contacted for authors and future members: Österreichische Gesellschaft für Herpetologie, c/o Naturhistorisches Museum, Burgring 7, A-1014 Wien.

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THE HERPETOLOGICAL JOURNAL

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(revised January 1992)

- The Herpetological Journal publishes a range of features concerned with reptile and amphibian biology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by a member of the editorial board); short notes; controversies, under 'Forum' (details available from the Editor); and book reviews. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance.
- 2. *Three* copies of all submissions, and illustrations, should be sent to the Editor. All papers will be subject to peer review by at least two referees
- 3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. Typesetting is greatly assisted if accepted manuscripts can be supplied on microcomputer diskettes. Authors are therefore strongly encouraged to produce manuscripts using a wordprocessor (preferably on a PC-compatible microcomputer).
- 4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of 5 words or less. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. Short notes (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.
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Bellairs, A. d'A. (1957). Reptiles. London: Hutchinson. Boycott, B. B. & Robins, M. W. (1961). The care of young redeared terrapins (Pseudemys scripta elegans) in the laboratory. British Journal of Herpetology 2, 206–210.

- Dunson, W. A. (1969a). Reptilian salt glands. In Exocrine glands, 83-101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.
- Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. American J. Physiol. 216, 995-1002.
- 9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
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