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FRONT COVER: Dendrophidion nuchale (P. J. Stafford)

## TROPHIC ECOLOGY AND REPRODUCTION IN THREE SPECIES OF NEOTROPICAL FOREST RACER (*DENDROPHIDION*; COLUBRIDAE)

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Aspects of ecology are described and compared for three species of the Neotropical colubrid genus Dendrophidion: D. nuchale, D. percarinatum and D. vinitor. These slender, racer-like snakes of Central American rainforests have overlapping distributions and similar, relatively specialized diets. Within each species, over 50% of prey items recovered from museum specimens were leptodactylid frogs. Dendrophidion vinitor is a small species that feeds almost entirely on these anurans (>90% by frequency), whereas D. nuchale and D. percarinatum are larger forms that in addition to frogs also eat lizards, mostly anoles (Polychrotidae). Sample numbers were limited and the dietary data insufficient for conclusive analysis, but niche separation based on this taxonomic difference in food habits - and also prey size (larger mean prey volume in D. nuchale) - may be important for these snakes in areas of co-occurrence. Reproductive data for D. percarinatum and D. vinitor in lower Central America suggest an extended or possibly continuous cycle and the production in individual females of more than one clutch per year. The intensity of reproduction in all three species, however, is likely to fluctuate with annual variation in rainfall and prey availability. Dendrophidion percarinatum shows a much higher frequency of tail breakage than D. nuchale or D. vinitor, suggesting that predation pressure in this species is relatively more intense.

Se describen aspectos de la ecología de tres especies de culebras neotropicales pertecientes al género Dendrophidion: D. nuchale, D. percarinatum y D. vinitor. Estas delgadas y rápidas culebras de los bosques tropicales de América Central, tienen una distribución solapada y dietas similares y relativamente especializadas. Para cada especie, más de un 50% de las presas recuperadas de especímenes de museos fueron ranas leptodactílidas. Dendrophidion vinitor es una culebra pequeña, que se alimenta casi exclusivamente de estos anuros (>90% en frecuencia), mientras que D. nuchale y D. percarinatum son especies de mayor tamaño, que a parte de ranas, también se alimentan de lagartijas, principalmente de anoles (Polychrotidae). Se contó con un número limitado de ejemplares, por lo que los datos sobre la dieta fueron insuficientes para un análisis concluyente, sin embargo, la separación de sus nichos basada en las diferencias de alimentación y tamaño de las presas (un mayor volumen de la presa en promedio en D. nuchale), pueden ser importantes para estas culebras en áreas donde co-ocurren. Datos reproductivos de D. percarinatum y D. vinitor en la parte sur de América Central sugieren un ciclo extenso o posiblemente continuo y en el caso de algunas hembras, más de una puesta por año. Sin embargo, la intensidad reproductora de las tres especies, posiblemente varíe con la precipitación anual y la disponibilidad de presas. Dendrophidion percarinatum muestra rotura de cola con una mayor frecuencia que D. nuchale o D. vinitor, lo que sugiere que esta especie sufre una más intensa presión por parte de sus predadores.

Key words: Central America, Colubridae, Dendrophidion, diet, ecology, reproduction, sympatry

#### INTRODUCTION

Snakes of the genus *Dendrophidion* are a distinctive group of Neotropical colubrids noted for their attenuate body-shape, large eyes, and great speed of movement. Eight species are currently recognized, with a combined geographic range extending from southern Mexico (*D. vinitor*) to the Guianas, northern Brazil and east-central Peru (*D. dendrophis*); a complex of populations in the southern Amazon basin of Bolivia and vicinity appears to represent a ninth, undescribed species (Lieb, 1988). Commonly known as 'forest racers', they are diurnal and mostly terrestrial inhabitants of low-moderate elevation rainforests, although several also occur in upland areas, and for *D. bivittatum* in the northern Andes there are admissible records from above 2300 m (Dunn, 1944).

Previous studies on *Dendrophidion* have clarified the taxonomic status, overall relationships, and distributions of species (Lieb, 1988), and summarized available data on the four known Central American forms (Lieb, 1991a,b,c, 1996). Our basic knowledge of these snakes, however, is marked by an otherwise distinct lack of in-

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formation, particularly with respect to their diet and life history patterns. In this paper I present a general account of morphology, food habits and reproduction in three *Dendrophidion* species from Central America and north-western South America – *D. nuchale* (W. Peters), *D. percarinatum* (Cope), and *D. vinitor* H. M. Smith – based on examinations of preserved museum specimens and records of field observations. The information enables some preliminary comparisons between the ecologies of these taxa, which occur widely in the region over similar elevational ranges, and in various combinations are not infrequently 'sympatric'.

Dendrophidion nuchale, percarinatum and vinitor are similar in overall morphology but attain different body sizes and are distinct also in features of colour pattern (for colour illustrations see Renjifo & Lundberg, 1999; Stafford & Meyer, 2000; Köhler, 2001; Savage, 2002). The largest is D. nuchale, adults of which may attain total lengths in excess of 1.5 m. Dendrophidion nuchale also has the most extensive distribution, ranging from east-central Guatemala and Belize, south through Honduras, Nicaragua, Costa Rica, and Panama, to northern Venezuela and the Pacific versants of Colombia and Ecuador (75-1585 m). Dendrophidion percarinatum is a moderately-sized species (<1.3 m) known mostly from lower Central America (Honduras to Colombia and western Ecuador, 4-1200 m), while D. vinitor, a smaller form (<1.1 m), occurs from southern Veracruz to Panama and the adjacent Chocoan area (15-1528 m). Data presented by Lieb (1988) suggest that D. nuchale and D. vinitor are closely related forms allied to the nominate South American D. dendrophis. As a group, these species are segregated from percarinatum and the remaining members of the genus by the more extensive development of dorsal scale keeling, differences in posterior dorsocaudal scale row reductions, and features of hemipenal morphology.

#### MATERIALS AND METHODS

In total, 41 D. nuchale, 58 D. percarinatum and 55 D. vinitor were examined. These included individuals from throughout the range of each species, but most originated from lower Central America, particularly north-eastern Costa Rica. All snakes were first sexed by inspection of the gonads through a mid-ventral incision (or in some males by the presence of everted hemipenes) and their date of collection, provenance, snout-vent length (SVL) and tail length (TL) recorded. In order to quantify any differences between the species in head and body proportions, and to determine whether there was a relationship between morphology and diet, the following additional measurements were also taken; mid-body circumference (MB-C, determined by wrapping a piece of tape around the snake's mid-body and measuring the length used), head length (HL, measured along the upper jaw to its point of articulation), head width (HW, measured at the angle of the jaw), head depth (HD, measured from a point directly above the eye), snout length (SL, measured from the anterior border of the eye to the front face of the rostral), and diameter of the eye (ED).

Approximately one half of the specimens within each species sample were then dissected to obtain diet and reproductive data; a small number of these were selected by palpating the abdomen for the presence of food, but the remainder (>95%) were selected on a wholly random basis. Prey items recovered from stomachs were counted, identified, and whenever possible their length (SVL), volume (determined by fluid displacement), mass, and orientation were also recorded. The sizes of more fully digested prey items were estimated by comparison with similar-sized intact specimens in the collection of the Natural History Museum (BMNH), and to reduce error in determining prey mass all spirit-preserved material was thoroughly drained before

TABLE 1. Comparisons of relative head and body measurements in Dendrophidion nuchale, D. percarinatum and D. vinitor, based
on the ten largest individuals examined (5 male and 5 female). Data are mean, SE and range (first three rows) and test results of
Mann-Whitney U comparisons (NS, $P > 0.05$ ; * $P < 0.05$ ; ** $P < 0.01$ ). See text for abbreviations.

Species	SVL/MBC	SVL/HL	HL/HW	HL/HD	HL/SL	HL/ED
D. nuchale	14.02±0.48 (11.98-16.14)	25.39±0.43 (23.0-27.04)	2.27±0.06 2.01-2.57)	2.84±0.04 (2.63-3.08)	3.42±0.06 (3.21-3.82)	4.73±0.02 (4.58-4.81)
D. percarinatum	14.01±0.21 (12.91-15.08)	26.12±0.33 (24.51-27.41)	2.17±0.02 (2.06-2.28)	2.84±0.06 (2.60-3.17)	3.62±0.06 (3.40-3.92)	4.8±0.05 (4.64-5.09)
D. vinitor	14.69±0.42 (11.86-16.32)	26.81±0.27 (25.35-27.90)	2.23±0.05 (2.04-2.48)	2.67±0.04 (2.50-2.84)	3.76±0.05 (3.54-4.00)	4.48±0.08 (3.93-4.92)
D. nuchale × D. percarinatum	<i>z</i> =0.03 NS	<i>z</i> =1.21 NS	<i>z</i> =1.21 NS	<i>z</i> =0 NS	<i>z</i> =2.31*	<i>z</i> = 1.74 NS
D. nuchale × D. vinitor	<i>z</i> =0.9 NS	z=2.41 *	<i>z</i> =0.45 NS	z=2.35 *	z=3.06 **	z=2.57 **
D. percarinatum × D. vinitor	<i>z</i> =1.59 NS	z=1.59 NS	z=1.02 NS	z=2.24 **	z=1.66 NS	z=2.95 **

	D. nuchale		D. per	carinatum	D. vinitor	
	male ( <i>n</i> =25)	female ( <i>n</i> =17)	male ( <i>n</i> =28)	female (n=27)	male ( <i>n</i> =31)	female $(n=25)$
Maximum SVL (cm)*	96.8	94.8	71.2	75.6	66.4	64.5
Mean adult SVL ±SE (cm)	78.7±3.44	74.8±3.73	64.4±1.31	67.4±1.35	60.0±1.20	57.8±1.10
Ratio mean adult SVL m/f (±SE)	) 1.05 (:	±0.03)	0.96 (±	5.0x10 <sup>-3</sup> )	1.04 (±	4.7x10⁻³)
Ratio TL/Tail L (range)	0.350-0.408	0.350-0.405	0.365-0.450	0.367-0.417	0.339-0.381	0.313-0.366
Ventrals*	153-175	156-174	149-169	152-169	149-168	155-167
Subcaudals*	138-163	132-157	141-163	143-151	111-127	110-126

TABLE 2. Body sizes and sexual dimorphism in *Dendrophidion nuchale*, *D. percarinatum* and *D. vinitor*. \*Includes selected data from Smith (1941) and Lieb (1988). TL, total length; Tail L, tail length.

weighing. Reproductive maturity was determined in females by the presence of ovarian follicles >5 mm diameter or oviducal eggs. Males were considered mature if the testes were enlarged and the vasa deferentia distinctly thickened. Finally, the numbers and dimensions of enlarged ovarian follicles and oviducal eggs were recorded in reproductive females. All measurements of less than 5 cm were made using digital calipers accurate to 0.1 mm.

#### RESULTS

#### MORPHOLOGY

Dendrophidion nuchale, D. percarinatum and D. vinitor are slender, attenuate-bodied snakes with rela-



FIG. 1. Regressions of tail length on SVL in *D. nuchale* (crosses and continuous line; y = 0.6764x - 29.391,  $R^2 = 0.9815$ ), *D. percarinatum* (circles and dashed line; y = 0.7726x - 23.183,  $R^2 = 0.9698$ ), and *D. vinitor* (squares and dotted line; y = 0.6064x - 22.836,  $R^2 = 0.9776$ ). Note proportionally longer tail of *D. percarinatum*.

tively long tails, short snouts, and large eyes. As a proportion of head length, the eye in *D. vinitor* is especially large, and *D. vinitor* also has a shorter snout, deeper head, and shorter tail compared with *nuchale* and *percarinatum* (Tables 1 and 2, Fig. 1). In other features of morphology the three species are relatively similar. Interspecific differences in body size (SVL), however, are marked (Table 2). *Dendrophidion nuchale* is much the largest, and for any given SVL in the sample studied, *D. nuchale* also had a significantly larger head. This difference is greatest with regard to *D. vinitor*, but was evident in comparisons between all three species (single-factor ANCOVA based on head length with SVL as the covariate,  $F_{2,122} = 41.07$ , P < 0.0005) and remains proportionally consistent with increasing SVL (Fig. 2).



Snout-vent length (mm)

FIG. 2. Relationship of head length and width to SVL in *D.* nuchale (crosses and continuous line), *D. percarinatum* (circles and dashed line) and *D. vinitor* (squares and dotted line). Note larger head of *D. nuchale*. The regression equations are, head length: y = 0.0286x + 8.6251,  $R^2 =$ 0.9408 (nuchale); y = 0.0269x + 8.0226,  $R^2 = 0.9635$ (percarinatum); and y = 0.0249x + 8.0073,  $R^2 = 0.9633$ (vinitor); head width y = 0.0128x + 3.8975,  $R^2 = 0.8855$ (nuchale); y = 0.0117x + 3.763,  $R^2 = 0.9174$  (percarinatum) and y = 0.0102x + 4.1712,  $R^2 = 0.8977$  (vinitor).

Prey category	D. nuchale (n=8/27)	D. percarinatum (n=12/23)	D. vinitor (n=13/25)
Frogs – unidentified spp.		3 / 15.8 /3	
Hyla spp.			1 / 4.2 / 1
Colostethus sp?			1/4.2/1
Eleutherodactylus spp.	7 / 63.6 / 5	8/42.1/5	19 / 79.2 / 9
Unidentified leptodactylids	2 / 18.2 / 2	2 / 10.5 /2	3 / 12.5 / 3
Lizards – unidentified spp.		1 / 5.3 / 1	
Norops spp.	2/18.2/2	4/21.1/4	
Cnemidophorus sp.		1 / 5.3 / 1	
Totals	11 / 100 / 9	19 / 100.1 / 16	24 / 100.1 / 14

TABLE 3. Prey types identified from stomachs of *Dendrophidion nuchale*, *D. percarinatum* and *D. vinitor*. Data are number of prey items, % total number of prey items (for that species) and frequency (number of snakes with that category of prey). n= proportion of specimens with food / total number of specimens examined for dietary data.

Dendrophidion percarinatum is conspicuous in having an exceptionally long tail, accounting in males for up to 45% of the total adult length (Table 2, Fig. 1). Based on the total number of specimens examined, D. percarinatum also showed a much higher incidence of broken tails than D. nuchale and D. vinitor (47% compared with 23% and 19% respectively). Frequency of tail breakage may be a useful indicator of predation pressure in snakes and also a potential indicator of differential predation (Zug et al., 1979; Henderson et al., 1981). Only the Costa Rican sample of D. percarinatum and D. vinitor contained sufficient numbers of individuals to draw comparisons between species in an area of sympatry, but the results were significant, indicating an appreciably greater level of predation in D. percarinatum (17/32 [53.2%] versus 6/29 [20.7%] in D. *vinitor*;  $\chi^2 = 7.28$ , df=1, *P*=0.007).

Sexual size differences (SVL) within the species were minimal, males averaging slightly larger than females in *D. nuchale* and *D. vinitor*, but smaller in *D. percarinatum* (Table 2). Differences between the sexes in tail length and abdominal scale counts were also relatively minor.

#### DIETS

Fifty-four identifiable food items were recovered from the stomachs of 8 D. nuchale, 12 D. percarinatum and 13 D. vinitor (Table 3). The most common prey in all three species were small frogs, predominantly of the genus Eleutherodactylus (Telmatobiinae; Leptodactylidae). These anurans comprised at least 63% and probably >75% (since most unidentified frogs had one or more characteristics associated with this group) of the total number of feeding records, and with the exception of a single hylid and Colostethus were the only prey type recorded for D. vinitor, whereas the stomachs of D. nuchale and D. percarinatum also contained lizards, mostly anoles (Polychrotidae). This taxonomic difference between species in composition of the diet was statistically significant (Fisher's exact tests=6.151, P=0.025 and 10.431, P=0.002 for each respective com-

parison), but sample numbers were small and the data too limited for definitive interpretation. In the relative proportions of frogs and lizards eaten by D. nuchale and D. percarinatum there was no apparent difference (Fisher's exact test=0.971, P=0.841). Dendrophidion nuchale and D. percarinatum of all size classes contained frogs, but the individuals that contained lizards were all mature adults over 480 mm SVL. This may again simply reflect a bias due to the small sample sizes, but it may also indicate an ontogenetic broadening of prey spectrum in these species. Various other items were found in the stomachs of D. percarinatum and D. vinitor, including a number of lizard eggs, a spider, and unidentified arthropods, but these were invariably associated with frog or lizard remains and hence were probably ingested secondarily. Lizard eggs, however, may occasionally be eaten by these snakes. A 512 mm SVL Dendrophidion bivittatum examined from SW Colombia (BMNH 1909.4.30.66) contained two fully shelled lizard eggs in its stomach but no other remains of prey, and predation on lizard eggs is not uncommon among other colubrids that feed on lizards, e.g. Drymobius margaritiferus (Sieb, 1984), Drymoluber dichrous (Martins & Oliveira, 1998).

Most prey items for which identification to species level (or species group) was possible were terrestrial or leaf-litter forms. Common prey species recorded for D. percarinatum included Eleutherodactylus bransfordii, E. fitzingerii, and the anoline lizard Norops limifrons. Several D. vinitor from Costa Rica had eaten E. bransfordii and members of the E. gollmeri group, and others from Mexico contained E. cf. lineatus, while specific prey records for D. nuchale included Eleutherodactylus laticeps (Belize), Ε. cf. conspicillatus (Ecuador) and Norops rodriguezii (Belize). Only two of the frogs recovered were arboreal, an eleutherodactyline with prominently expanded toe pads (species unknown) that had been eaten by a D. nuchale, and a transforming metamorph of Hyla ebraccata contained by a D. vinitor (C. Guyer, pers. data). The number of prey items in stomachs ranged from 1-4, with 38% of

the specimens (all three species combined) containing >1. Most of the lizards for which direction of ingestion could be determined had been swallowed head-first, but a significant proportion of the frogs had been consumed instead by the 'tail' (48%). There was also an apparent relationship between direction of ingestion and the number of frogs eaten; in snakes that contained only a single frog, almost all (94%) had been ingested head-first, whereas regardless of size, 70% of frogs eaten by snakes that contained two or more items had been ingested tail-first.

The size range of prey was greatest in D. nuchale, a probable correlate of the larger head and body size attained by this species; mean prey size (vol.) in D. nuchale was 2.71 cm<sup>3</sup> ( $\pm$ 1.48, range 0.4-11.5, n=7), compared to 1.33 ( $\pm 0.25$ , range 0.3-3.5, n=14) in D. percarinatum and 0.49 (±0.15, range 0.15-1.30, n=9) in D. vinitor. Notwithstanding the limited sample numbers, D. nuchale also contained food less frequently than did D. percarinatum and D. vinitor (Table 3;  $\chi^2$ =8.90, df=1, P < 0.005 and  $\chi^2 = 4.13$ , df=1, P < 0.05 for each respective comparison). All three species had fed mostly on relatively small prey and only an occasional larger item was found in their stomachs. For example, a 36.5 gm (498 mm SVL) D. vinitor contained three juvenile Eleutherodactylus sp., of which the largest had a mass of less than 1.2 gm (MR <3.3%). An 89.3 gm (639 mm SVL) D. percarinatum had eaten two Eleutherodactylus fitzingeri that were 1.73 (MR 1.9%) and 1.44 gms (MR 1.6%). The largest single prey item relative to snake body length was a 34.8 mm SVL Eleutherodactylus sp. found in a 308 mm SVL D. nuchale, for which a prey/ predator mass ratio of 24.2% was calculated.

Feeding activity occurs throughout the year, but primarily during the wet season (May-December over most of the species' combined Central American range). Within each species, several females that contained food also contained ovulatory-sized follicles or shelled eggs, indicating that females do not habitually abstain from feeding when gravid; among snakes in general, a reduction or complete cessation of feeding activity in gravid females is more typical (Shine, 1979).

#### REPRODUCTION

Clutch sizes within the three species relative to female body length (SVL) were small, averaging 6.3  $(\pm 0.75, range 5-8, n=4)$  in *D. nuchale*, 4.9  $(\pm 0.16, range 4-6, n=14)$  in *D. percarinatum* and 4.2  $(\pm 0.25, range 3-5, n=10)$  in *D. vinitor*. In the two species for which sufficient data were available (*percarinatum* and *vinitor*), there was a positive correlation between clutch size and SVL (Fig. 3), but in *vinitor* the strength of this relationship is not great, and within both species the presence of small clutches in relatively large individuals suggests that factors other than body size (e.g. feeding success, overall health) may have a significant controlling influence on fecundity. Mean lengths of the largest shelled oviducal eggs ranged from 29.8 mm in *D*. nuchale (range 28.4-31.2, n=5) to 25.1 (range 22.3-29.8, n=6) in *D. percarinatum* and 18.2 (range 17.1-19.4, n=10) in *D. vinitor*.

For most localities the reproductive data were insufficient to draw conclusions on the frequency or timing of reproduction. Females with developing follicles or oviducal eggs were present in samples from throughout the range of each species, but no individual locality had adequate representation of specimens for all months of the year. Combining localities in Costa Rica for *D. percarinatum* and *D. vinitor*, however, permits at least some measure of insight into the reproductive phenology of snakes in this area. Within *D. percarinatum*, enlarged follicles (>5 mm) were recorded for specimens collected between January and November, while females with oviducal eggs were found in May, July and



FIG. 3. Relationship of clutch size to female SVL in *D.* percarinatum (circles and dashed line; y = 0.0027x + 3.2098,  $R^2 = 0.0526$ ) and *D. vinitor* (rhomboids and dotted line; y = 0.0013x + 3.5016,  $R^2 = 0.0218$ ).



FIG. 4. Monthly variation in size of the largest ovarian follicle in female *D. percarinatum* (circles) and *D. vinitor* (rhomboids) from Costa Rica. Hollow symbols indicate oviducal eggs.

October (Fig. 4). Ovaries of D. vinitor contained enlarged follicles over a shorter period (April-August), but eggs were present in specimens with collection dates ranging from early March to mid-December. Hatchlings of D. percarinatum were collected in August and December, and others of D. vinitor in January, June and July. The irregular nature of this pattern suggests an extended or possibly continuous reproductive cycle in Costa Rican D. percarinatum and D. vinitor. Oviposition and hatching appear to be coincident mostly with the wet season, but are not restricted to this time. The overall length of the breeding cycle and lack of a welldefined single period of vitellogenesis further implies the production in some females of more than one clutch per year. Another possible explanation is that vitellogenesis is protracted over several months and reproduction occurs in alternate years, as suspected for Yucatán populations of the morphologically similar Dryadophis melanolomus (Censky & McCoy, 1988). However, the relatively large proportion of females in the sample that were reproductive (i.e. gravid, with enlarged follicles or oviducal eggs: 85% [11/13] in percarinatum and 82% [9/11] in vinitor) is more suggestive of 'multiple' annual cycles, and this is further supported by the presence in some individuals of follicles at different stages of enlargement. One 554 mm SVL D. vinitor collected in mid-April contained follicles of three size classes (15.4-17.2 mm, n=3; 8.6-8.7 mm, n=3; and 4.3-4.5 mm, n=11), each presumably representing a discrete and separate clutch. In addition, clutch size in all three species is relatively small, this being consistent with other data (Zug et al., 1979), indicating that selective pressure may exist among tropical snakes for fewer or larger eggs per clutch and more clutches per year.

Body length (SVL) measurements of the smallest individuals examined provide an indication of size at hatching; for D. nuchale this measurement was 245 mm, for D. percarinatum 185 mm, and for D. vinitor 182 mm. Smaller body sizes may have been recorded had sample numbers been larger, but the presence of yolk sac scars on the smallest individuals of percarinatum and vinitor, combined with differences between the species in relative egg size, suggest that the figures are a close if not precise estimate of actual size at hatching. The smallest females exhibiting reproductive activity had SVL measurements of 536 mm (nuchale), 441 mm (percarinatum), and 294 mm (vinitor). Males reach sexual maturity at similar or larger sizes, with lengths of 556 (nuchale), 473 (percarinatum), and 364 mm (vinitor) recorded for the smallest individuals with enlarged testes and thickened sperm ducts.

#### DISCUSSION

Dendrophidion nuchale, percarinatum and vinitor are diurnal, essentially terrestrial snakes apparently adapted for rapid movement and visually-orientated predation. The large eye is a particularly distinctive feature and probably evolved as a specific adaptation for searching out and following prey that moves quickly and erratically; this has been suggested previously by Dixon *et al.* (1993) for species of the derived genus *Chironius*, many of which occur in similar habitats and also feed chiefly on *Eleutherodactylus*. Large eye size in *Dendrophidion* may be further related to the difficulties of visual hunting at ground level in closed-canopy forests (i.e., low angle of view, reduced light), and this may also explain why the HL/ED ratio in these snakes is greater than that in many arboreal colubrids, including certain nocturnal forms (for comparisons see Henderson & Binder, 1980).

Body sizes (SVL) differ considerably among the three species, but not between sexes within species. In D. nuchale and D. vinitor adult males were generally larger than females, whereas in D. percarinatum the largest individuals examined were females. Statistical comparisons of these relative size differences were not significant (Mann-Whitney U-tests, P>0.30). Information on maximum body size in the sexes of other species of Dendrophidion is meagre; for D. dendrophis, however, males are reported to attain total lengths of 1142 mm (Gasc & Rodrigues, 1980), while females reach 1183 mm (tail 44.9-52.2% of total length) (Martins & Oliveira, 1998). The approximate equivalence of males and females in body size is a frequent correlate of male combat in snakes (Shine, 1978, 1994) and offers incidental evidence for the occurrence of such behaviour in Dendrophidion. There are no published reports of physical combat between males of the three species discussed here or others within the genus, but this may simply reflect the lack of behavioural observations on these snakes. Males of some related taxa do show combat (e.g., Chironius bicarinatus, Almeida-Santos & Marques, 2002; C. carinatus, see Starace, 1998).

#### PREDATION INTENSITY

Differences between the three species in the number of individuals with damaged tails suggest that predation pressure in D. percarinatum is relatively more intense. More than half of the D. percarinatum examined showed evidence of tail injury, compared with less than 25% in D. nuchale and D. vinitor. A possible explanation for this difference is that D. percarinatum may forage in a wider range of habitats than D. nuchale or D. vinitor, including less densely forested environments with a more open canopy (see discussion of foraging ecology). The tail in this species may also be more fragile and easily broken (or more liberally discarded). In the absence of any quantitative observations, however, a direct explanation of this phenomenon must await further study. An interesting feature of the tail in D. nuchale is its distinct reddish colour, often more vivid in adults (disruptive/aposematic?).

High predation pressure in *Dendrophidion* may explain why these and many other diurnal snakes sleep in vegetation at night (Martins, 1993; Martins & Oliveira, 1998). At La Selva in Costa Rica, many more D.

*percarinatum* and *D. vinitor* can be observed at night than during the day, sleeping in shrubs and bushes approximately 2 metres from the ground (C. Lieb, pers. comm.).

#### DIETS AND FORAGING ECOLOGY

The presence of a small and taxonomically limited range of organisms in the diets of D. nuchale, D. percarinatum and D. vinitor suggests that the species are relatively specialized in their feeding habits. Over 75% of prey items were small frogs of the family Leptodactylidae (>80% of these in one genus, Eleutherodactylus) and D. vinitor appears to feed almost exclusively on these anurans. Although dietary overlap was substantial in terms of the main prey type consumed, however, differences between the species in composition are seemingly apparent, with D. nuchale and D. percarinatum feeding also on lizards. This feature of the diet is not in itself unique or especially remarkable but may explain the coexistence in some areas of D. vinitor with D. nuchale and D. percarinatum, particularly in the absence of any clear differences among the species in habitat occupancy, foraging mode, or the times of day/year when foraging occurs. Division of prey on the basis of size may also be important for these snakes, as indicated by the larger body size, head size, and overall mean prey size in D. nuchale. Possible competition between syntopic Dendrophidion, however, as well as between these snakes and other species with similar habits, may presumably be expected only if resource availability was limiting.

That no Anolis or other non-anuran prey items were recovered from D. vinitor is strong evidence of anurophagy but does not necessarily imply active selection of frogs by this species. As noted for some elapids (Shine, 1977), species that feed on frogs but which live in habitats where lizards are also found often eat both prey types, possibly because the nutritional benefits of eating all potential prey items whenever they are encountered far outweigh the operative 'costs' of capturing and handling them. The fact that anoles are ubiquitous throughout much of Central America and ofabundant in the same microhabitats as ten Eleutherodactylus, however, contends that if indeed D. vinitor does eat lizards, this prey type should appear frequently in its diet. Why this is not reflected by the data, albeit limited due to the small sample numbers, may therefore be significant. Specialist frog predators that forage in habitats where lizards also occur are not uncommon among Neotropical colubrids (e.g. members of the Xenodontini), and this trait may be ultimately due to phylogenetic constraints. Lee (2000) referred to a D. vinitor that ate lizards (Norops sp.) in captivity.

Accounts of food habits published previously for *D.* nuchale, *D.* percarinatum and *D.* vinitor are generally consistent with the results of this study, although no evidence was found of toads in the diet of nuchale, as indicated by Roze (1952), or rodents and other small mammals (Lancini & Kornacker, 1989; Pérez-Santos &

Moreno, 1988, 1991). Test et al. (1966) reported on a captive D. nuchale from Venezuela (as percarinatum) that ate Prostherapis (= Mannophryne) trinitatis, M. neblina, and Eleutherodactylus cornutus maussi, noting that the same snake refused a toad (Bufo granulosus) and gecko (Gonatodes taniae). For D. percarinatum in specific prey items have included Panama Eleutherodactylus diastema, frogs of the genus Leptodactylus, and other (unidentified) frogs (Sexton & Heatwole, 1965). All three species are characterized by Savage (2002) as frog-eating forms. Information available for D. dendrophis (Cunha & Nascimento, 1978; Dixon and Soini, 1986; Duellman, 1978; Nascimento et al., 1987; Vanzolini, 1986) suggests that frogs are an important component in the diet of this South American species as well, a variety of different taxa having been recorded (Adenomera, Eleutherodactlyus, Colostethus, Hyla and Scinax). Cunha & Nascimento (1978) stated that in addition to frogs dendrophis feeds on insect larvae, and - according to Abuys (1982) and Starace (1998) - this species will also eat lizards and birds, an observation disputed by Martins (2000).

Predator-prey size relationships inferred for the three species are comparable with those demonstrated by Martins & Oliveira (1998) for *D. dendrophis* in Central Amazonia. Individuals of this species, with total lengths ranging from 946-1128 mm (17-62.5 g) were found to have also fed predominantly on small frogs, usually less than 10% of their mass (range <3-18%). Similar ratios were recorded by Sieb (1984) for two other Neotropical racers that feed on frogs and lizards, *Drymobius chloroticus* and *D. margaritiferus*. Mean prey/predator mass ratios for these species were 4.1% and 5.3% respectively, and the largest prey item, contained by a *D. margaritiferus*, was 28.6% the mass of the adult snake.

The stomach content data are to some extent informative also about foraging habits in D. nuchale, percarinatum and vinitor. Of the 35+ prey organisms identified to species level (or morphotypic group in the case of some unidentified leptodactylids), only two were arboreal, confirming the predominantly terrestrial habits of these snakes; Savage (2002), however, indicates that D. vinitor will readily climb into bushes or trees when foraging or to escape predation, and all three species may be commonly observed sleeping above ground at night. The preponderance of *Eleutherodactylus* further indicates that prey-searching activities are restricted mostly to areas where there is extensive canopy cover (e.g. see Guyer, 1990 and individual species accounts in Lynch and Myers, 1983; Savage, 1987, 2002). Some foraging by D. percarinatum, however, may occur in more open environments, as suggested by the presence in its diet of *Leptodactylus* frogs and lizards of the genus Cnemidophorus. Often, species in these genera are found in habitats that are relatively exposed and devoid of significant tree cover (see Lee, 1996; Wright, 1993). Dendrophidion are diurnal snakes and the two genera of lizards identified from stomachs are also strictly diurnal. In contrast, the frogs are active mostly at night. The

greater part of the diet would thus appear to consist of prey that are effectively inactive and possibly also hidden from the snakes when they are foraging, many *Eleutherodactylus* being procryptic and emerging from shelter only at night or, if by day, during/following rain (Duellman, 1978; Toft & Duellman, 1979). Detection and capture of these frogs may be further complicated by their erratic leaping behaviour and the habit in some species when attempting to evade predators of adopting a motionless, low crouching posture (e.g. *E. bransfordii*; C. Lieb, pers. comm.).

Field observations indicate that prey is located by active searching. An adult *D. nuchale* and a juvenile *D. vinitor* observed moving slowly across leaf litter in dense forest (Belize and Costa Rica) would pause at intervals to push their snouts into the substrate, and Test *et al.* (1966) similarly described individuals of *D. nuchale* from Venezuela (as *percarinatum*) moving through leaf litter 'in a manner suggestive of foraging'. The head is often held well above the ground, probably to aid detection of prey and/or maintain visual contact with flushed and escaping prey.

#### REPRODUCTION

Reproductive data for D. percarinatum and D. vinitor from Costa Rica suggest a nearly continuous cycle with the production in individual females of more than one clutch per year. Most adult-sized females from localities in this area contained enlarged vitellogenic follicles or oviducal eggs, and a small number contained both. Because the majority of gravid females were collected during the wettest period of the year (May-December) however, the possibility of a more seasonally-orientated cycle cannot be ruled out, particularly in view of the fact that samples consisted of individuals collected over many years (50+), thus obscuring annual variation in season length. It is perhaps significant, however, that the dry season in north-eastern Costa Rica is not severe (Hammel, 1990), and a common prey species of Dendrophidion in this area, Eleutherodactylus bransfordii, also appears to reproduce nearly year-round (Donnelly, 1999). Food availability has been implicated as a major determinant of reproductive frequency in snakes (Vitt, 1983; Seigel & Ford, 1987) and in certain species the intensity of reproduction from year to year has been shown to fluctuate widely as a direct result of annual variation in prey abundance (e.g. Andrén & Nilson, 1983). Given the clear importance of frogs in the diets of D. nuchale, D. percarinatum and D. vinitor, and the often high correlation in tropical regions between anuran activity and rainfall (see Neill, 1962; Henderson & Hoevers, 1977; and individual species accounts in Lee, 1996; Savage, 2002), it is thus likely that reproduction during prolonged dry periods is less frequent.

Data from other localities within lower Central America (Nicaragua, Panama, Chocoan Colombia) collectively showed a similar trend towards more or less

continuous reproduction in D. percarinatum and D. vinitor. Egg-laying by individuals of D. nuchale during the non-rainy season in Venezuela suggests that reproductive activity in snakes from this area may follow a similar pattern (Test et al., 1966). An interpretation of the reproductive cycles in other populations of these three snakes, however, is not possible without the benefit of additional data. The potential of a species for modifying its pattern at different localities has been indicated in a number of tropical colubrids (e.g. Zug et al., 1979), and owing to the pronounced seasonality of rainfall in certain areas, particularly northern Central America, a seasonal cycle may well be found in some populations. In keeping with this is the observation that all three hatchlings of D. vinitor from Mexico were collected between August and October, corresponding to the middle part of the wet season in this area, as were the only two hatchlings of D. nuchale (from Belize and Guatemala).

Clutch sizes in Dendrophidion nuchale, percarinatum and vinitor are generally consistent with other fecundity data published for the snakes of this genus. For a 633 mm SVL D. brunneum, Kuch & Freire (1993) reported a clutch size of six, and another examined by myself with an SVL of 668 mm contained four. Mean egg length (unshelled) in the latter clutch was 25.6 mm (x 8.7 wide). A 512 mm SVL D. bivittatum in the collection of the BMNH (1909.4.30.66; Colombia) also contains four eggs (shelled), the average length of which is 33.4 mm (x 10.5). For D. dendrophis in Surinam, Abuys (1982) reported a clutch size range of 12-15. Limited data available for this species in other parts of its range, however, would seem to contradict this observation; Duellman (1978) refers to an individual from Ecuador that contained six eggs (30.2 mm in length), and for two others in Central Amazonia Martins & Oliveira (1998) recorded clutch sizes of four and six, the latter from a female having an SVL of 571 mm.

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Museum). George Zug and Ronald Crombie confirmed SVL measurements and provided other data for a number of D. vinitor paratypes in the collection of the U.S. National Museum, and Richard Lehtinen provided similar information for a paratype at the University of Michigan's Museum of Zoology. Measurements for a number of Nicaraguan specimens were contributed by Gunther Köhler (Forschungsinstitut und Naturmuseum Senckenberg). Craig Guyer (Auburn University) and · Carl Lieb (University of Texas at El Paso) gave freely of their observational data on *Dendrophidion* in the field, and for help regarding access to a number of Costa Rican specimens I am indebted also to Jay Savage. Robert Henderson (Milwaukee Public Museum), Marcío Martins (Instituto de Biociências, Universidad de São Paulo) and Wolfgang Wüster (University of Wales) provided helpful comments on the original draft version of this manuscript, and the Spanish summarization was kindly prepared by Mamen Peña.

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#### APPENDIX 1

SPECIMENS EXAMINED

#### Dendrophidion nuchale

BELIZE - Cavo District: 1.6 km W Baldy Sibun (LSUMZ 8901); Dos (Las) Cuevas, 500 m (LSUMZ 8902); Sibun Hill (LSUMZ 8903); Cuxta Bani, upper Raspaculo River, 425 m (PJS field nos. 9703, 9704). Stann Creek District: Middlesex, 125 m (UCM 25708, 25794, 25805, 25806, 25846, 25847, 25874). GUATE-MALA - Alta Verapaz: btw Coban and Lanquin (BMNH 64.1.26.4-5). Izabal: Sierra de Las Minas, Los Amateas, Aldea Vista Hermosa, 1000 m (KU 190916). HONDURAS - Atlántida: Quebrada de Oro (ROM 19970). NICARAGUA - no specific locality (USNM 14220). COSTA RICA - Puntarenas: Finca Helechales, 1050 m (LSUMZ 11636); 4-6 km S San Vito de Jaba, Finca Las Cruces, 1200 m (LACM 148556); 6.4 km S San Vito de Java, Finca Las Cruces, 1219 m (LACM 148553). PANAMÁ – Bocas Del Toro: Bocas Del Toro Boquete trail (MCZ 22210). Darien: Laguna, 820 m (KU 75681). COLOMBIA - Caldas: Pueblo Rico, Santa Cecilia, Pacific side, 800 m (FMNH 54939). Chocó: Cãno Decordo, btw Cucurrupí and Noanomá, on Río San Juan, ca. 100 m (CAS 119591, 119604); Pueblo Rico, slopes of San Juan River, SW Colombia, 5200 ft (BMNH 1910.7.11.24). Valle de Cauca: Cisneros, 1100 m (FMNH 43738, 43741). ECUADOR – Paramba, 3500 ft (BMNH 98.4.28.59); St. Javier (BMNH 1901.3.29.28). Carchi: Maldonado, 1410 m (KU 179499). NW Ecuador: Bulim, 160 ft (BMNH 1901.8.3.4); Rio Sapayo, 450 ft (BMNH 1902.7.29.17). PERU - Cuzco: Tono (FMNH 229571). VENEZUELA

Aragua: Rancho Grande (UMMZ 142678); Rancho Grande, nr biological station (UMMZ 122355); Rancho Grande Biological Station, Portachelo Pass (CAS 139477); Rancho Grande, Telegraph Trial nr Portachelo Pass (UMMZ 142679). Guarico: 5 km NE La Colonia guard station, Parque Guatopo, 3250 ft (TCWC 59025). Miranda: 37.4 km N Altagracia, 1400 ft (TCWC 59020); 26.2 km N Altagracia (TCWC 59020); 27 km N Altagracia, 2200 ft (TCWC 59024); 2 km E Hwy 12, 26 km N Altagracia, 3000 ft (TCWC 59026).

#### Dendrophidion percarinatum

No data (FMNH 154510, 154516). HONDURAS -Atlántida: Lancetilla (MCZ 29677). NICARAGUA -Comoapa (MCZ 9550); Río Mico, 10 mi above Recero (UMMZ 79764). Santo Domingo: Chontales Mines, 2000 ft (BMNH 94.10.1.18). Zelaya: 7 mi above Rama, Río Siguia (UMMZ 79767). COSTA RICA - no specific locality (LACM 148579, 148584). Alajuela: Venado, 9 km N Arenal, 252 m (LACM 148580). Cartago: Bataan (KU 30998); Turrialba, 605 m (LACM 148577). Heredia: Finca La Selva, 40 m (LACM 148585); Finca La Selva, 60 m (LACM 148586); Finca La Selva, 2.4 km SE Puerto Viejo, 60 m (LACM 148558, 148560). Limón: Barra del Colorado, 4 m (LACM 148587); vic Cahuita, ca 4 m (LACM 148582); Los Diamantes (KU 30997); Pandora, 17 m (LACM 148581); Sixaola, Talamanca, 800 ft? (BMNH 1956.1.6.48). Puntarenas: Cajón (BMNH 1978.767); Finca Las Cruces, nr San Vito de Jaba on road to Villa Neily, 4 km, 1200 m (LACM 148566); 0.4 km W of Motel Bella Vista, Golfito, 15 m (LACM 148564); Golfito, 12 m (LACM 148568); 6.3 km S of Pan Am Hwy on Golfito road, 7 m (LACM 148567); Gromaco, between Río Coton and Río Coto Brus at juncture, 480 m (LACM 148569); La Lola, 39 m (LACM 148578); Palmar (KU 31948); vic Río Disciplina, 1680 ft? (LACM 148588); 2 km S entrada Palmar Sur, 15 m (LACM 148592); Rincón de Osa, 5 m (KU 102506); 3.5 km WSW Rincón de Osa, 40 m (LACM 148562); vic Rincón de Osa, 20 m (LACM 148563); 3 km WSW Rincón de Osa, 0.5-1 km S Osa Field Station, 4060 ft (LACM 148571); 4 km SW Rincón de Osa, Holdridge Trail, 60 m (LACM 148575); 5 km SW Rincón de Osa, 10 m (LACM 148570); 7.5 km SW Rincón de Osa, Quebrada Rayo, 20 m (LACM 148576); San Luis River at footbridge, ca. 740 m (LACM 148559). PANAMÁ – Canal Zone: Barro Colorado Island (KU 80589); Barro Colorado Island, Wheeler Trail (UMMZ 63762); Fort Clayton (KU 107649); Fort Randolph (MCZ 20552); Gatun (FMNH 16760); Hydrographic Station, Salamanca (MCZ 39978); Juan Mina (MCZ 26646). Chirikuí (BMNH 94.5.17.8-9). Darien: Cana, 500 m (KU107651); Ortiga site (FMNH 170152); Río Tiura at Río Mono, 130 m (KU 107653, 107655); Tacarcuna, 550 m (KU 75677). Veraguas: Isla Gobernadora (KU 107648). COLOMBIA - Antioquia: Uraba, Río Currulao (FMNH 63761, 63773); Villa Arteaga (FMNH

78118). *Chocó*: Piña Lisa, Condoto, 300 ft (BMNH 1913.11.12.40).

#### Dendrophidion vinitor

MÉXICO – no specific locality (BMNH 60.6.17.13); Forest at Cascapel, upper Uzpanapa River, Isthmus of Tehuantepec (BMNH 1936.6.6.8). Oaxaca: no specific locality (UCM 39911-39912); Donaji, Mije District (UCM 44481); La Gloria (FMNH 126555); La Gloria, 1500 ft (FMNH 126554); Río Negro (Grijua), Juchitrán (UCM 41162). Veracruz: 60 km SW Jesus Carranza (KU 23965); nr Coyame, 1400 ft (UMMZ 111450); Volcán San Martin, nr base (UMMZ 122767); SE slope Volcán San Martin, ca. 2600 ft (UMMZ 121145). GUA-TEMALA - Alta Verapaz: btw Coban and Lanquin (BMNH 64.1.26.21). NICARAGUA - Matagalpa (MCZ 9561). Atlantico Sur: Cara de Mono, 50 m (KU 112974). Santo Domingo: Chontales Mines, 2000 ft (BMNH 94.10.1.19-20). COSTA RICA - Alajuela: Poco Sol de La Tigre, 540 m (LACM 148601). Cartago: 2.5 km N Pavones, nr Río Revantazon, 700 m (LACM 148594); Pavones, ca. Turrialba (KU 140055). Guanacaste: Cacao Biological Station, 729-1528 m (LACM 148589); Volcán Orosí, trail from Maritza Biological Station to Cerro Cacao, 750 m (PJS field no. 9618). Heredia: Finca de Selva, 60 m (LACM 148616); Finca La Selva, 2.4 km S Puerto Viejo, 60 m (LACM 148605, 148619); Finca La Selva, 2.4 km SE Puerto Viejo, 60 m (LACM 148591, 148609); Finca La Selva, research trail at forest plot, 40 m (LACM 148593); Finca La Selva, river road, 40 m (LACM 148595, 148597, 148611); Finca La Selva, river road at cacao plot, 40 m (LACM 148598); Finca La Selva, cacao plot nr. Quebrada Experimental (LACM 148603); Finca La Selva, Quebrada Esquina at SE boundary, 100 m (LACM 148604); Finca La Selva, south loop trail (LACM 148621). Limon: Pandora, 50 m (LACM 148618); Puerto Viejo (KU 35639). Puntarenas: 4 km S San Vito de Jaba, 1200-1300 m (LACM 148614); 6.4 km S San Vito de Jaba, Finca Las Cruces, 1219 m (LACM 148596); Finca Las Cruces, nr San Vito de Jaba on road to villa, 4 km S San Vito, 1200 m (LACM 148599, 148613, 148617); Las Cruces field station at San Vito de Java, 1100 m (LACM 148606); Las Cruces, San Vito (LACM 148608); Las Cruces, down toward Rio Jaba, 1100 m (LACM 148615); Finca Loma Linda, 2 km SSW Canas Gordas, 1170 m (LACM 148590, 148620). PANAMÁ – Pequeni-Esperanza ridge, nr head R Pequina, 2 mi E of Panama R (MCZ 42782); Pequeni-Esperanza ridge, 2 mi E of Panama R (MCZ 42783). Bocas Del Toro: Almirante (KU 80223); 11 km NW Almirante, 600 ft (FMNH 153653, 154038-154039). Darien: Laguna, 820 m (KU 75680); San Blas Territory; border of Darien, Summit site (FMNH 170138). COLOMBIA \_\_\_\_ Chocó: Quebrado, Bochorama, Loma de Encarnacion on Right bank (LACM 45443).

## REPRODUCTIVE BIOLOGY OF THE VIVIPAROUS SEA SNAKE EMYDOCEPHALUS IJIMAE (REPTILIA: ELAPIDAE: HYDROPHIINAE) UNDER A SEASONAL ENVIRONMENT IN THE NORTHERN HEMISPHERE

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> Reproductive traits of Emydocephalus ijimae were examined on the basis of specimens from shallow waters around the central Ryukyus, Japan. Sampling was carried out from December 1979 until November 1980 (with the exception of September), and yielded a total of 240 specimens. Gonadal examinations revealed that males and females mature at 550-600 mm and 500 - 550 mm snout-vent length (SVL), respectively. We therefore regarded female snakes > 550 mm SVL and male snakes >500 mm SVL as adults. Mean length of the largest ovarian follicles in the monthly adult female sample increased gradually from July to March, and rapidly from March to April, and then swiftly decreased from April to June. Oviducal eggs occurred only in samples from May to November, although the occurrence of one gravid female in early January was recently reported. Possible neonates (i.e. juveniles as large as the largest embryos [280-320 mm in SVL]) were found from November to January. These data suggest that ovulation occurs from May to June and parturition from November to January after 6-8 months of gestation. Of 19 adult females collected in June, ten (52.6%) were gravid, whereas the remainder had neither oviducal eggs nor enlarged ovarian follicles close to ovulation. Likewise, both gravid and nongravid females were observed in each of the July-November samples, although their sample sizes were much smaller (4-8) and frequencies of gravid individuals varied considerably (0-50%). It is likely that the overall frequency of reproduction in individual females is biennial or even less frequent. Clutch size varied from 1 to 4 eggs, and showed no significant correlation with maternal body size (as represented by SVL or BW). In adult males, on the other hand, gonadal index (total mass of gonads  $\times 100$ /body mass) increased from May to November, and largely decreased from November to April. Present results indicate that the reproductive activities of both male and female E. ijimae are synchronized and seasonal, as in some other lower latitude marine snakes.

Key words: biennial reproduction, clutch size, reproductive cycle, Ryukyu Archipelago

#### INTRODUCTION

The venomous sea snakes of the family Elapidae (sensu McDowell, 1987) consist of two distinct clades that most likely represent independent marine invasions (Keogh *et al.*, 1998; Heatwole, 1999). Of these clades, one consisting of so-called sea kraits (the subfamily Laticaudinae) is characterized by oviparous reproduction, whereas members of the other clade (the subfamily Hydrophiinae) are invariably viviparous (Heatwole, 1999).

The elapid sea snakes have been considered as interesting subjects for studying the process and mechanism of adaptations to the marine life by ectothermic amniotes, and a number of research projects have thus been carried out in this context (see reviews by Dunson, 1975; Heatwole, 1999). Nevertheless, relatively little is known of the ecology of this group of sea snakes. With respect to reproductive biology, most studies have been carried out on populations from low latitudes in the Southern Hemisphere and equatorial region (Voris & Jayne, 1979; Lemen & Voris, 1981; Burns, 1985; Ward, 2001; Fry *et al.*, 2001). For the reproduction of sea snakes in the distinctly seasonal region of the Northern Hemisphere, quantitative data are available only for one oviparous species, *Laticauda semifasciata* (Kuwabara *et al.*, 1990; Tu *et al.*, 1990).

Emydocephalus ijimae is a viviparous hydrophiine species inhabiting coral reefs in the East China Sea (Nakamura & Ueno, 1963; David & Ineich, 1999), an area with distinct seasonal fluctuations in water temperature (Fig. 1) and representing the northernmost extremity of a range of coastal-water dwelling sea snakes (Toriba, 1994). Along with its congener (E. annulatus) and another species of a different genus from Australasian and South-east Asian waters (Aipysurus eydouxi), E. ijimae is known to feed exclusively on fish eggs (Voris, 1966; Voris & Voris, 1983; Heatwole, 1999). This suggests that this sea snake plays a peculiar role in the coral ecosystem (Voris, 1972). Nevertheless, very little is known of other ecological aspects of E. ijimae. With respect to reproduction, published information is limited to records of three females collected

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FIG. 1. Monthly averages of water temperature in Okinawajima, the central Ryukyus, measured at a depth of 1 m. Data obtained from 1978 to 1996 by the National Sea Level Monitoring Centre of Japan were used. Horizontal and vertical lines, and vertical bars represent means, ranges, and standard deviations, respectively.

from the central Ryukyus in October, November, and January that had 3-4 embryos (Moriguchi, 1991; Uehara, 1993).

In this study, we analyse the reproductive traits of *E. ijimae* from the central Ryukyus on the basis of samples obtained from almost a complete year of study. We then compare the reproductive pattern of this species with those of other sea snakes hitherto studied.

#### MATERIALS AND METHODS

Sampling was carried out in all months from December 1979 until November 1980, except for September. Sea snakes found in shallow waters (<10 m) around Sesokojima ( $26^{\circ}37-39'N$ ,  $127^{\circ}51-53'E$ ) and Zamamijima Islands ( $26^{\circ}13-15'N$ ,  $127^{\circ}17-20'E$ ) of the central Ryukyus, were captured by hand and euthanized in the laboratory.

Specimens were then measured for snout-vent length (SVL) to the nearest 5 mm, using a flexible tape measure for individuals greater than 400 mm SVL, or to the nearest 1 mm by rigid ruler for individuals less than 400 mm SVL. Body weight (BW) was taken to the nearest 0.5 g using an electronic balance for each individual. After these measurements, ovaries and oviducts (female), or testes and epididymides (male), were extracted from each specimen by abdominal autopsy, and were fixed in the Bouin's solution (Lee, 1950).

For each male, gonads were weighed to the nearest 0.01 g by electronic balance, and gonadal index, defined as total mass of gonads  $\times$  100/total body mass, was calculated accordingly. Male gonads were then dehydrated, embedded in paraffin, and sectioned at 8--10  $\mu$ m. Sections were stained with Delafield haematoxylin-eosin, and were observed under a light microscope.

For each female, diameter of the largest ovarian follicle was measured to the nearest 0.1 mm with dial calipers. Oviducal eggs, when present, were counted and embryos, when evident, were also measured for SVL to the nearest 1 mm using a bar scale. Developmental stages of embryos followed definitions by Hubert & Dufaure (1968).

#### RESULTS

#### SIZE AT MATURITY

Some females between 550 and 600 mm SVL showed signs of sexual maturity, but others exhibited none (Fig. 2). In the following analyses, we therefore treated females greater than 550 mm (SVL) as adults. Of the ten females collected in April, seven, with a SVL larger than 600 mm had ovarian follicles larger than 18 mm in length. Another female measuring 575 mm SVL, had two distinctly enlarged ovarian follicles (greater than 44 mm in length), whereas the two remaining specimens, 545 and 585 mm (SVL) respectively, had follicles less than 12 mm length. In the other monthly samples, all females greater than 600 mm (SVL) also had ovarian follicles greater than 12 mm in length, oviducal eggs or embryos, or flaccid oviducts (an indication of recent embryos), whereas those less than 550 mm (SVL) exhibited none of these features.

Microscopic examination of gonadal sections revealed that most males greater than 500 mm (SVL) had distinct seminiferous tubules with sperms, spermatids, or large hollows that had most likely been occupied by



FIG. 2. Size distribution, based on sount-vent length (SVL, in mm), in monthly samples of male (left) and female (right) *Emydocephalus ijimae* from the central Ryukyus, Japan. Individuals were categorized as mature (open), immature (filled), and possible neonates (stippled). The numbers to the left and right above each month's column are male and female sample sizes, respectively.

recently ejected sperms. In contrast, in testes of all males less than 500 mm (SVL) seminiferous tubules were not recognized, or were recognized but with no evidence of spermatogenesis (Fig. 2). These suggest that male *E. ijimae* mature at around 500 mm (SVL). In the following analyses, we thus treated males greater than 500 mm (SVL) as adults.

#### **OVARIAN FOLLICLES IN ADULT FEMALES**

The monthly fluctuation in the length of the largest follicle (LFL) in adult females is shown in Fig. 3. The monthly mean was smallest in July (6.83 mm), increasing gradually to March (29.50 mm), and rapidly to April (47.38 mm). The value dropped rapidly in May (17.50 mm), more slowly to June (9.71 mm) and finally to July (see above). The standard deviation of LFL varied extensively among the monthly samples, being low in the July-November samples (0.96–1.72 mm), moderate in the January-March and June samples (3.41–6.60 mm), and largest in the April (15.84 mm) and May (16.14 mm) samples. In the latter two samples, the LFL ranged from 11.5 to 60.5 mm and from 4.5 to 52.5 mm, respectively (Fig. 3).

Gravid females were found only in the samples from May (42.8%), June (52.6%), July (50%), August (50%) and November (28.6%). All four adult females collected in October were not gravid. No significant differences were recognized in mean of LFL (mean±SD; range) between the gravid  $(14.17\pm2.52 \text{ mm}: 11.5-16.5 \text{ mm}: n=3)$ and non-gravid adult females (20.00±22.29 mm; 4.5-52.5 mm: n=4) in the May sample (Student's t-test using log-transformed values: t=0.16, P>0.05; two tailed variances ratio test: F=35.94, P>0.05). In the June sample, no significant differences were found in mean of LFL between the gravid  $(9.10\pm5.56 \text{ mm}; 4.5-20.5 \text{ mm};)$ n=10) and the non-gravid adult females (10.39±4.76) mm; 5.5–20.5 mm; n=9; t=1.43, P>0.05; F=1.36, P>0.05). Differences were not evident in either the mean or the variance of LFL between the gravid and nongravid adult females in each of the July, August, and



FIG. 3. Annual pattern of largest follicle length in adult female *Emydocephalus ijimae* from the central Ryukyus, Japan. Horizontal and vertical lines and vertical bars represent means, ranges, and standard deviations, respectively. The numbers above are sample sizes. Rectangles and circles represent individual data for gravid and nongravid females, respectively.

November samples, although their sample sizes were too small for statistical analyses (Fig. 3).

#### OVIDUCAL EGGS AND EMBRYOS

The clutch size in gravid females (see above) varied from 1 to 4 (mean=2.74, SD=0.75, n=20). This range covers the values previously reported for three gravid females from the central Ryukyus (3-4: Moriguchi, 1991; Uehara, 1993). Analysis of pooled data from our specimens and those from previous reports of Moriguchi (1991) and Uehara (1993) revealed that the clutch size was unrelated to female body size as represented by body weight (t=1.69, P>0.05; Fig. 4) or SVL (t=0.60, P>0.05).

Of a total of eight oviducal eggs from the three gravid females in the May sample, four had blastoderms, but the remaining four, including three comprising a single clutch, did not show any evidence of development. A total of 28 oviducal eggs were obtained from the ten gravid females in the June sample, of which six (two clutches) were not fixed well and thus were not examined in detail. Of the remaining 22 eggs, 16 showed embryos at stages 26-30 of Hubert & Dufaure (1968), whereas the remaining six did not show any evidence of development at all. The three gravid females collected in July had a total of five oviducal eggs, all possessing embryos at stages 34-38. Of a total of ten oviducal eggs from the three gravid females in the August sample, four - all in the same clutch - had embryos at stages 39-41, whereas five others were at stages 36-38. The remaining egg showed no evidence of development at all. All five eggs from the two gravid females in the November sample seemed to have fully developed embryos with SVLs ranging from 310 to 322 mm (mean=315.4, SD=4.72).

#### **GONADAL CYCLE IN MALES**

The gonadal index in adult males showed a considerable monthly fluctuation, with a minimum in June and a maximum in November. Values in the remaining months varied between these extremes. Gonadal indices



FIG. 4. Relationship between body size (represented by body weight in log scale) and clutch size of gravid female *Emydocephalus ijimae* from the central Ryukyus, Japan.



FIG. 5. Annual pattern of male gonadal index (percentage of body weight). Horizontal and vertical lines represent medians and ranges, respectively.

in October and January were slightly smaller than the values in August and February, respectively (Fig. 5).

Microscopic examinations of sections showed that the seminiferous tubules of testes were filled with sperm (characterized by distinct tails) in all adult males collected in December and three of the six adult males in November. In males collected from January to March, the seminiferous tubules also contained sperm but in decreasing densities. The tubules in all adult males from April to October and in the remaining three of the November males lacked sperm. Seminiferous tubules in all August and October males, as well as in the three November males that lacked sperm, were filled with dense spermatocytes and spermatids medially. In contrast, the tubules in adult males collected from April to July exhibited more or less prominent voids and many fewer cells in lumens.

#### APPEARANCE OF JUVENILES IN MONTHLY SAMPLES

Juveniles smaller than 400 mm (SVL) were collected only in the winter months of December and January. These samples included one and two juveniles whose respective SVLs did not reach 300 mm (i.e. 280 mm, and 280 and 297 mm: Fig. 2). These values are smaller than those of the well-developed embryos possessed by the two gravid November females (see above). They are within the range of SVLs of six neonates reported by Moriguchi (1991) and Uehara (1993) (266–342 mm: mean=301.5; SD=30.6).

#### DISCUSSION

# SEXUAL SIZE DIMORPHISM AND ANNUAL REPRODUCTIVE OUTPUTS

Greer (1997) listed the maximum SVL of *E. ijimae* as 750 mm. Our results, though, indicate that females of this species very often exceed 750 mm, and sometimes even reache 900 mm (Fig. 2). Heatwole (1999), on the other hand, suggested that there was no sexual size dimorphism (SSD) in *E. ijimae*. However, because the minimum (555 mm), mean (726.2 mm), and maximum (900 mm) SVLs in adult females were larger than in males (510 mm, 626.5 mm, and 745 mm; Fig. 2), it is obvious that this sea snake exhibits a SSD like the majority of other sea snake species (Heatwole, 1999; Fry *et* 

al., 2001; Ineich & Laboute, 2002) or of snakes in general that have been studied to date (Shine, 1993).

For snakes, such SSD is often considered a consequence of selection that favours larger females due to their greater fecundity (review by Shine, 1993, 1994). Indeed, a majority of snakes - including more than two thirds of the marine species - are known to show statistically significant correlations between female body size and clutch size (Lemen & Voris, 1981; Seigel & Ford, 1987; Greer, 1997). In E. ijimae, however, no significant correlation was recognized between these variables. Moreover, of the adult females collected in June (a post-ovulation season), gravid individuals (SVL: mean=750.5 mm, 605-835 mm; n=10) were even smaller than the non-gravid females (mean=810.0 mm, 765-885 mm; n=9) (ANOVA: F=5.07, P<0.05). It is, therefore, likely that the observed SSD in the present species is not a direct consequence of selection for greater fecundity. Patterns of SSD in the other congeneric species, E. annulatus, remain uncertain, although Guinea (1996) mentioned that in one observed mating pair of this species the female was larger in SVL than the male. Since most other hydrophiine sea snakes - including a species of Aipysurus (the putative sister group of Emydocephalus: Voris, 1977; Rasmussen, 2002) - also have larger females (Heatwole, 1999; Burns & Heatwole, 2000), it is probable that the observed SSD in E. ijimae actually represents phylogenetic conservatism rather than the consequence of proximate selection (Shine, 1994). Further population studies, using the mark-recapture technique, are needed to verify this conclusion, especially by examining the influence of body size upon the survivorship of gravid females (Shine, 1993, 1994). Mark-recapture studies are also needed to clarify the proximate mechanisms responsible for the observed SSD (e.g. Burns & Heatwole, 2000).

Lemen & Voris (1981), based on the analyses of various reproductive parameters in hydrophiines and other marine snakes from Malaysia, recognized several reproductive patterns that are considered in the context of rand K-selection. Such a divergence in the reproductive pattern seems to be prominent also in the hydrophiines of Australia (Ward, 2001; also see pertinent tables in Greer, 1997). The mean clutch size in gravid females of E. ijimae (2.74) is one of the smallest of the hydrophiines so far examined (Greer, 1997; Ward, 2001: Fry et al., 2001). Furthermore, considering that only 16 adult females (45.7%) out of 35 collected during the gestation period (i.e. from June to October: see below) were gravid, it is highly likely that an adult female reproduces biennially or even less frequently like a few other hydrophiine species (Burns, 1985; Ward, 2001). Thus, the mean annual reproductive output of an adult female E. ijimae seems to be even less than 1.4, and this suggests that this seasnake is a typical K-strategist. Mean relative reproductive effort per embryo (10.3%: sensu Lemen & Voris, 1981), calculated from data for two females and their neonates in Moriguchi (1991) and

Uehara (1993), is close to the highest known value for hydrophines (10.9% for *Hydrophis fasciatus*: Lemen & Voris, 1981), and this further supports the hypothesis of *E. ijimae* being a K-strategist.

#### ANNUAL REPRODUCTIVE PATTERN IN FEMALES

Rapid reduction in mean length of the largest ovarian follicles from April to May, along with the complete absence of oviducal eggs in the April sample and their presence in a part of the May sample, indicates that ovulation commences in May. Furthermore, the presence of a non-gravid female with large ovarian follicles in the May sample - and the complete absence of such females in the June and subsequent samples - suggest that, in all females scheduled to breed in a given year, ovulation is completed no later than June (Fig. 3). On the other hand, the largest follicle lengths in non-gravid females are significantly greater in the February-April samples than in the June-August samples, with a very slight range overlap (ANOVA: F=17.68, P<0.001). This, as well as the absence of apparent differences in this variable between gravid and non-gravid females in each of the latter (Fig. 3), suggests that in spring, vitellogenesis in ovarian follicles occurs almost in all adult females, and that in non-reproductive females, vitellogenic follicles are subjected to yolk re-absorption, instead of ovulation, from April to June.

Aldridge (1979) recognized two seasonal patterns in the secondary vitellogenesis of ovarian follicles in temperate zone snakes: type I, as characterized by a rapid secondary vitellogenesis only in the spring; and type II, by commencement of secondary vitellogenesis shortly after ovulation. A seasonal pattern of secondary vitellogenesis in the central Ryukyu population of E. ijimae, illustrated by an increase in ovarian follicle length shortly after ovulation (i.e., in July: Fig. 3), seems to belong to type II. However, it differs from the typical type II pattern in lacking an apparent cessation of vitellogenesis during the cold season (from December to March: see Fig. 1), unlike many temperate zone terrestrial snakes (Aldridge, 1979) and another sea snake, Aipysurus laevis, from subtropical Australian waters (22°-22°10'S) (Burns, 1985). Aipysurus laevis studied by Burns (1985) also differs from E. ijimae of the central Ryukyus in showing a clear dichotomy of adult females into reproductive and non-reproductive individuals in a given year (indicated by a marked difference in the largest follicle length), more than one month before commencement of ovulation. Considering that nutrition condition usually plays a crucial role in the commencement or cessation of vitellogenesis in snakes (Aldridge, 1979; Saint Girons, 1982; Seigel & Ford, 1987), it is probable that the differences in vitellogenic patterns between the two subtropical reef-dwelling sea snakes may be attributable to differences in seasonal energetic patterns resulting from those in their feeding habits (Voris & Voris, 1983). Rapid increase of spawning by coral reef fishes with an increase in water

temperature in spring (Thresher, 1984) may account for the "delayed decision" regarding ovulation by female E. *ijimae*.

Our data, and those from the literature (Moriguchi, 1991; Uehara, 1993) indicate that in E. ijimae of the central Ryukyus parturition occurs from November to January. This, along with the timing of ovulation, suggests that the gestation period ranges from six to eight months. This value is similar to those estimated for other sea snakes also showing biennial or less frequent reproduction (Aipysurus laevis: six months; and Hydrophis elegans: seven months [Burns, 1985; Ward, 2001]), and is larger than those for sea snakes that reproduce annually (Lapemis curtus: five months; Enhydrina schistosa: three months [Voris & Jayne, 1979; Ward, 2001]), as well as for most terrestrial live-bearers (3-4 months: Shine, 1977; Tinkle & Gibbons, 1977). This may support the idea that a decrease in frequency of reproduction in some aquatic snakes involves an extension of gestation period, which necessitates a female having a long non-breeding interval after breeding to restore nutrition (e.g. Burns, 1985; Ward, 2001). In E. *ijimae*, however, the success of spring food intake may be crucial, as mentioned above, to the occurrence of an individual's ovulation in a given year, rather than the presence or absence of gestation in the preceding year.

#### ANNUAL REPRODUCTIVE PATTERN IN MALES

Spermatogenic cycles in male temperate snakes are usually classified into two types, post-nuptial and prenuptial, on the basis of timing of maximum spermatogenetic activity in relation to the ovulation season (Volsoe, 1944). Of these, the post-nuptial type, showing testicular weight peak in autumn, is much more common than the pre-nuptial type in which maximum testis mass is achieved in early spring, just before ovulation in conspecific females (Seigel & Ford, 1987). In tropical snakes, on the other hand, spermatogenesis is generally aseasonal or essentially pre-nuptial (Saint Girons & Pfeffer, 1971; Fitch, 1982; Vitt, 1983), and Seigel & Ford (1987) doubted the presence of the postnuptial tropical cycle.

Of the elapid sea snakes, members of Ladicauda so far studied, including subtropical East Asian populations of L. semifasciata, exhibited no significant seasonal variation in testis mass (Gorman et al., 1981; Bacolod, 1983; Tu et al., 1990). In contrast, testis mass in three hydrophiines from tropical waters (Enhydrina schistosa from Malaysia, and Lapemis curtus and Hydrophis elegans from northern Australia: Voris & Jayne, 1979; Ward, 2001) showed a typical pre-nuptial pattern with its peak appearing in 2–3 months before ovulation.

*Emydocephalus ijimae* from the subtropical Ryukyus showed a prominent seasonal variation in testis mass like these three tropical hydrophiines. Even so, the peak of testis mass in *E. ijimae* (November: Fig. 5) precedes ovulation (May to June: Fig. 3) by no less than six months, suggesting that the spermatogenic pattern in this species is post-nuptial. Considering that the two northern Australian species showed the testis mass peak in May (a month corresponding to late autumn in the higher latitude of the Southern Hemisphere) and ovulation in August (late winter), it is probable that the annual reproductive pattern of *E. ijimae* has been formed under the influence of an extended cold season upon females as a result of dispersal from the tropical region to higher latitudes. This scenario is comparable to that hypothesized for the evolution of a seasonal reproductive pattern in some viperid snakes in North America (Aldridge & Duvall, 2002).

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## OVIPOSITION BEHAVIOUR AND VULNERABILITY OF EGGS TO PREDATION IN FOUR NEWT SPECIES (GENUS *TRITURUS*)

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Most animals develop some kind of parental care in order to protect eggs or offspring from predation. Female newts (genus *Triturus*) protect eggs from predators by wrapping them individually in plant leaves. We studied oviposition characteristics of four newt species inhabiting the northern Iberian Peninsula (marbled newt, *Triturus marmoratus*; alpine newt, *T. alpestris*; palmate newt, *T. helveticus* and Bosca's newt, *T. boscai*). All of these species are able to wrap their eggs in aquatic plants in laboratory experiments, but – whereas *T. marmoratus*, *T. alpestris* and *T. helveticus* wrapped more than 90% of their eggs – *T. boscai* covered only half of the eggs completely with leaves. *T. boscai* is found in running waters more frequently than the other species, and lays larger eggs relative to female size, as is typical of running water urodeles. A parallel experiment exposing newt eggs to predation by larvae of the dragonfly *Aeshna cyanea*, demonstrated the protective value of wrapping behaviour. About half of the unwrapped eggs were consumed, whereas protected eggs remained almost unattacked.

Key words: Aeshnidae, egg-laying, Odonata, parental care, Urodela

#### INTRODUCTION

Amphibians show a great diversity of reproductive modes ranging from the deposition of masses of eggs in ponds to viviparity (Duellman & Trueb, 1986). The development of each reproductive mode is associated with different degrees of exposure of eggs and larvae to environmental factors such as predation, competition and desiccation. Amphibian larvae are well known to develop antipredator strategies (Sih, 1987; Alford, 1999), but eggs are more vulnerable to predation and other potential risks due to their immobility. In contrast to those of other salamanders, newt eggs (genus Triturus) are not known to contain unpalatable or toxic substances (Ward & Sexton, 1981), but female newts attach eggs individually to aquatic plants, wrapping these eggs by means of adhesive substances on the egg membranes, as reported by Díaz-Paniagua (1989) for Triturus (marmoratus) pygmaeus, and Miaud (1994b) for T. alpestris and T. helveticus. Wrapped eggs are inaccessible to the majority of predators, such as aquatic invertebrates or adult newts, and therefore experience reduced predation rates (Miaud, 1993).

The present study examines oviposition behaviour in four newt species inhabiting the northern Iberian Peninsula (marbled newt, *Triturus marmoratus*; alpine newt, *T. alpestris*; palmate newt, *T. helveticus* and Bosca's newt, *T. boscai*), and also experimentally tests for the effect of wrapping behaviour on egg survival in the presence of dragonfly larvae, *Aeshna cyanea*, one of

the top predators found in ponds and other temporal aquatic habitats in the study area. Previous studies with other dragonfly species (Richards & Bull, 1990) indicated that predatory larvae detect the eggs by tactile cues, so wrapping eggs in leaves could prevent dragonflies detecting their presence. *A. cyanea* has also been reported to alter the behaviour and development of newt larvae (Van Buskirk & Schmidt, 2000; Schmidt & Van Buskirk, 2001).

#### MATERIALS AND METHODS

During the 2000 and 2001 reproductive seasons, adult females of four newt species (T. marmoratus, n=32; T. alpestris, n=13; T. helveticus, n=44; T. boscai, n=55) were collected in several pools and cattle-watering tanks in Asturias (northern Spain) and transferred to the laboratory. Females were placed for five days at 17°C and LD 12:12 photoperiod in individual plastic containers (18 cm in diameter) that held one artificial oviposition support consisting of nine cloth strips (10 x 0.8 cm) suspended from a float of polystyrene foam plate ( $8 \times 5 \times 1$  cm). Eggs were removed from the strips twice a day and placed for 24 hr in a drying chamber at 50°C until the mass remained constant. Dry egg mass was recorded to the nearest 0.0001g (number of eggs: T. marmoratus, n=1379; T. alpestris, n=269; T. helveticus, n=1961; T. boscai, n=609). We recorded female wrapping behaviour by placing newts in the same type of plastic containers filled with tap water and *Glyceria* sp. leaves taken from nearby ponds. This type of vegetation was present in the localities of capture and was frequently used by newts (T. cristatus, T. alpestris and T. marmoratus) in experiments developed by Miaud (1995) studying the selection of plants during newt oviposition. Natural vegetation was used to develop the experiments in realistic conditions. Oviposition was controlled every two days for a total of ten days per female. Only females that laid at least 15 eggs were considered in the experiment (numbers of females: T.

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marmoratus, n=18; T. alpestris, n=20; T. helveticus, n=21; T. boscai, n=13). Eggs were classified as wrapped if they were completely covered by folds of the leaves or unwrapped if they were uncovered (number of eggs: T. marmoratus, n=683; T. alpestris, n=897; T. helveticus, n=898; T. boscai, n=260). The effect of wrapping behaviour on egg predation by dragonfly larvae was investigated in a 24 hr experiment conducted in plastic containers (18 cm in diameter) filled with 0.4 litre of water. Half of the containers received ten eggs wrapped with naturally vegetation, whereas the other half received ten unwrapped eggs. Wrapped eggs were selected from large samples of eggs so that the degree of wrapping was the same between species, i.e. only eggs completely covered with leaves were used. Unwrapped eggs were obtained from naturally unwrapped eggs if possible, and in the other cases by the careful removal of the vegetation covering wrapped eggs. This egg manipulation has been described by Miaud (1994a) as not affecting the survival of the embryos. Late instar Aeshna cyanea dragonfly larvae were collected from local water bodies and allowed to acclimatize to laboratory conditions for three days. Dragonflies used in the trials were starved for three days before the experiments to minimize the effect of satiation on predator performance. Each predator was used only once during the experiments. Trials for both treatments were repeated 15 times for each species. Total egg-mass consumption by Aeshna larvae in 'unwrapped' trials was calculated by multiplying the number of eggs consumed in each trial by the dry egg mass for each species, obtained as stated above. After the experiments all the dragonflies, newt females and the remainder of the eggs were released in their original locations.

One-way ANOVA's and Scheffé post-hoc tests were used to test for differences in female size (snout-vent length) and in dry egg mass between the four newt spe-

TABLE 1. Summary of female size and characteristics of the eggs laid by Triturus species. All values are presented as mean  $\pm$  SE, with range in parentheses.

Female SVL (mm)	Egg dry mass (mg)	% wrapped eggs
T. marmoratus		
82.95±1.07	2.1±0.05	92.47±1.53
(68.28-96.31)	(1.5-2.7)	(78.57-100)
T. al pestris		
56.40±0.68	1.6±0.04	96.81±0.72
(53.03-62.02)	(1.4-2.0)	(88.88-100)
T. helveticus		
42.91±0.37	0.9±0.02	91.25±1.37
(38.01-47.98)	(0.6-1.2)	(75.47-100)
T. boscai		
42.81±0.38	1.7±0.03	45.81±7.55
(38.00-51.01)	(1.2-2.4)	(5.26-100)

cies. Differences in oviposition tactics (mean percentage of wrapped or unwrapped eggs per female) and unwrapped egg survival between species were analysed using a Kruskal-Wallis test and Mann-Whitney tests for post-hoc paired comparisons. The effect of oviposition mode on egg predation by *Aeshna* was tested using a Mann-Whitney test. Differences in total egg mass consumption were tested with a Kruskal-Wallis test. Deviation from normality was tested with a Shapiro-Wilk test and homogeneity of variance with a Bartlett-Box test.

#### RESULTS

There were significant differences in female SVL among species (ANOVA:  $F_{3,140}$ =958.95, P<0.001; Scheffé test: T. marmoratus > T. alpestris > T. helveticus = T. boscai; Table 1). Dry egg mass differs significantly among species ( $F_{3,140}$ =176.71, P<0.001), revealing Scheffé post-hoc test differences between all the species except for T. alpestris and T. boscai (T. marmoratus > T. boscai = T. alpestris > T. helveticus; Table 1). Oviposition tactics differed between species (Kruskal-Wallis test:  $H_3$ =32.153, P<0.001; Table 1), with T. alpestris having a significantly higher percentage of eggs wrapped with the vegetation than the other species (Mann-Whitney tests: T. mar-T. alp: U<sub>18,20</sub>=89, P=0.007; T.alp-T.helv:  $U_{20,21}=73$ , P<0.001; T.alp-T.bosc:  $U_{20,13}=17$ , P<0.001). No differences in percentage of wrapped eggs were found between T. marmoratus and T. helveticus ( $U_{18,21}=158.5, P=0.389$ ), whereas T. boscai differed from the other species and had only a half of their eggs wrapped (T.mar-T.bosc:  $U_{1813}$ =19.5, P<0.001; T.helv-T.bosc:  $U_{2113}$ =25, P<0.001). When newt eggs were exposed to Aeshna larvae predation, egg survival was positively influenced by wrapping (U<sub>60.60</sub>=557.5, P<0.001; Fig. 1). Differences in unwrapped eggs survival were found only between T.



FIG. 1. Effect of oviposition mode (wrapped or unwrapped egg) on the percentage of surviving eggs (mean + SE) after 24 hrs of exposition to larval dragonfly, *Aeshna cyanea*, predation.

marmoratus and T. alpestris ( $U_{15,15}$ =43, P=0.003). Total egg mass consumption by Aeshna presented marginally significant differences between species ( $H_3$ =7.62, P=0.054), being higher for T. alpestris (11.62±1.37 mg). Differences using Mann-Whitney tests were obtained only between T. alpestris and the two species with lower egg mass (T. marmoratus  $U_{15,15}$ =64, P=0.041 and T. helveticus  $U_{15,15}$ =35, P=0.001).

#### DISCUSSION

The results of this study revealed that wrapping behaviour is common in all the species considered. To our knowledge, this study provides the first data on wrapping behaviour in T. boscai, which - contrary to other species - wraps only a half of eggs in leaves. This species also lays eggs that are twice the size of those laid by a similar-sized species (T. helveticus), and is the only species frequently found in streams during the reproductive season. This reflects the pattern found in 74 salamander species by Kaplan & Salthe (1979), who observed that egg size was smaller in relation to female size in pond breeders than in those species breeding in running waters. A relatively large egg size could present difficulties in terms of egg manipulation in T. boscai females, affecting the wrapping sequence of eggs with plant leaves and consequently the percentage of eggs protected. T. boscai eggs can be found in natural habitats unwrapped or adhering to the underside of rocks, behaviour rarely observed in the other three species. Percentages of wrapped eggs observed for T. alpestris and T. helveticus are higher than those reported by Miaud (1994a) in previous experiments in which only 75% of the eggs were wrapped with the leaves.

Wrapping behaviour reduces algal infection and UV-B-damaging effects in Triturus eggs (Marco et al., 2001), but the most frequently reported function was related to protecting eggs from predators (Miaud, 1993, 1994a). Both vertebrate and invertebrate predators have been reported to attack and consume amphibian eggs causing a significant reduction in reproductive success (Henrikson, 1990; Miaud, 1993; Axelsson et al., 1997; Richter, 2000; Monello & Wright, 2001). Our results showed that the wrapping behaviour developed by female newts is highly effective in protecting eggs from Aeshna larvae predation. Aeshna larvae eat about a half of the unwrapped eggs whereas wrapped eggs did not suffer noticeable mortality. T. marmoratus, the species that laid bigger eggs, experienced the lowest percentage of egg consumption, but this is unlikely to be an effect of predator satiation because A. cyanea larvae consumed higher amounts (total dry egg mass) of T. alpestris and T. boscai eggs. Differential egg consumption could be due to differences between species in egg characteristics such as presence of toxic compounds or variation in chemical cues emitted by eggs. Experiments developed by Miaud (1993; 1994a) in order to study the protective effect of newt egg-wrapping behaviour found that only adult Dytiscus marginalis beetles consumed all the wrapped eggs, whereas the addition of other predators

(six arthropods, one gastropod and three amphibian species) did not affect egg survival. Furthermore, after one week in natural habitats no unwrapped eggs survived, whereas 20-54% of the wrapped eggs were still alive (Miaud, 1994*a*). In this study, predatory larvae were observed moving along the leaves where eggs are attached, searching for and identifying eggs using their antennae before eating them. So, wrapped eggs seem to be undetectable by the tactile sensory capacities of *A. cyanea*.

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## GEOGRAPHICAL DISTRIBUTION OF THE ENDEMIC SARDINIAN BROOK SALAMANDER, *EUPROCTUS PLATYCEPHALUS*, AND IMPLICATIONS FOR ITS CONSERVATION

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The Sardinian brook salamander, *Euproctus platycephalus*, is a cryptically coloured urodele found in streams, springs and pools in the main mountain systems of Sardinia, and is classified as critically endangered by IUCN. General reviews of the mountainous range where salamanders occur are numerous, but very few field-based distribution studies exist on this endemic species. Through a field and questionnaire survey, conducted between 1999 and 2001, we report a first attempt to increase data on the present distribution of *E. platycephalus*. A total of 14 localities where Sardinian salamanders are represented by apparently stable and in some cases abundant populations have been identified, as well as 30 sites where species presence has been recorded after 1991. Some 11 historical sites were identified which are no longer inhabited by the species. The implications of this distributional study for the conservation of the species and for the realization of an updated atlas are discussed.

Key words: amphibian decline, island endemic, range, Sardinian mountain newt

#### INTRODUCTION

The genus *Euproctus* (Urodela, Amphibia) consists of three endemic species. The Corsican brook salamander *E. montanus* is found on the island of Corsica and the Pyrenean brook salamander *E. asper* lives in the Pyrenees between France and Spain. The Sardinian salamander *E. platycephalus* is a slender, cryptically coloured endemic that inhabits pools and streams in the mountains of Sardinia. The conservation status of the three *Euproctus* species is listed as 'strictly protected fauna species' within the Bern Convention (1998). *E. platycephalus* is classified by IUCN as critically endangered, on the basis of its endemism and of an estimated population reduction of 80% over the last 10 years (IUCN, 2000).

Habitat loss could be one of the main threats to Sardinian salamanders, due to a long period of drought over the island (which caused a water deficit of -46.6% compared to the island's water requirements in 2000: Regione Sardegna 2000), resulting in small rivers and streams being completely or partially dry during the summer months. Remaining salamander habitats have become fragmented and sometimes threatened by anthropogenic disturbance, pollution and eutrophication. Predation and/or competition due to the introduction of non-native species, such as *Salmo trutta*, which have been implicated as a threat to other salamanders (Read, 1998; Tyler *et al.*, 1998; Knapp & Matthews, 2000), are further contributing factors that threaten the long-term survival of the species.

This salamander is known to live in the eastern part of Sardinia, in the main mountain systems: Limbara in the north, Gennargentu in the centre, and Sette Fratelli, Gerrei and Sarrabus in the south (Colomo, 1999). Alcher (1975) undertook a detailed field investigation listing a total of 45 sites where the species' presence was recorded, as adults or larvae. Puddu *et al.* (1988) published a general distribution map of the species in which its range basically overlaps with the mountainous areas of the island. Other distribution surveys and bibliographic sources do not add any information to the picture already described by these authors (Bruno, 1980; Rimpp, 1998).

Knowing the distribution of a particular species is a key issue in studies of theoretical and applied ecology, biodiversity and metapopulation biology (Cowley *et al.*, 2000). Besides being a fundamental goal in ecology, describing and explaining the distribution of endangered species has major significance for their conservation (Beebee, 1996). There is still little information concerning amphibian distributions and their relevance to the conservation management of threatened or declining populations. These field-based surveys should be combined with attempts to identify critical distribution determinants for a particular species.

Some widespread amphibians such as Triturus species, Rana temporaria and Bufo calamita in Britain, and endemics such as Chioglossa lusitanica in Portugal, have been extensively studied and their distribution documented with finely-scaled maps (Beebee, 1996; Teixeira et al., 2001). Another example is given by Delaguerre & Cheylan (1992), who present a detailed atlas of the Corsican herpetofauna, in which E. montanus distribution is described. Although the distribution map is not confirmed by recent field survey, it gives fundamental information for further studies. Many other amphibian species, some of them rare or endangered (such as the Sardinian salamander), need similar high-resolution distribution studies.

This paper presents an assessment of the distribution of *E. platycephalus*, using data collected during a field

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survey across the geographic range of the species over three years of research, conducted to identify locations that currently hold salamander populations. Reports of apparent population declines in the species are discussed, and information on its geographical distribution is used to assess potential threats to its persistence and long-term survival in various parts of its range.

#### **METHODS**

#### FIELDWORK SEASONS

Distribution data were collected during fieldwork seasons in 1999, 2000 and 2001. Fieldwork usually started in mid-April and finished in late July or August. This generally corresponded with the main breeding season of the species (Puddu *et al.*, 1988). Spring in Sardinia is usually mild and sunny with low precipitation (Delitala *et al.*, 2000). With summer approaching, water in the stream-beds diminishes gradually until most of the streams consist of a number of pools, either isolated or connected by very small water channels.

The 1999 field season focused on documenting the large scale distribution and typical habitat of the animals. At the end of it, six study sites were identified throughout the eastern part of the island (south, centre and north) and five sites surveyed in the south-west. During the 2000 field season, 14 sites were visited, including the six already known, and a questionnaire was distributed to forestry stations. In 2001, all known sites were re-visited, and 18 new sites (four in the south-west and 14 in the rest of the island) were surveyed, most of these suggested by replies to the Forestali questionnaire.

#### FORESTALI QUESTIONNAIRE

The Corpo Forestale e di Vigilanza Ambientale is a regional body in charge of controlling Sardinian territory, water courses and forests (equivalent to a forestry service). The island territory is divided into a number of districts, each one under the control of a forest station. The area is extensively patrolled by 'Forestali' workers, who usually have an excellent knowledge of the local flora and fauna and are able to give accounts of salamander presence or absence. The questionnaire was distributed to 79 forest stations all over the island in July 2000, in order to collect records of salamander distribution (Table 1). A coloured photograph and a description of the species were supplied too. As there is only one other urodele found in Sardinia (the cave salamander *Speleomantes* sp.) which occupies a different habitat from *E. platycephalus*, forest station accounts were considered highly reliable.

#### **SELECTION OF SURVEY SITES**

The distribution survey was designed to identify streams supporting salamander populations at present, covering as evenly as possible the three areas of the eastern part of the island: south, centre and north. Survey sites were selected by combining three main sources of information: personal field trips to various sites during the fieldwork seasons following the suggestions of local people and exploration of the territory; the collection of replies to the *E. platycephalus* questionnaire; literature reviews (Alcher, 1975; Puddu et al., 1988; Schenk et al., 1995; Rimpp 1998). Out of 55 distribution survey sites, 51% were visited during the field seasons (with local collaborators and forest station workers, or on our own initiative) and the remaining 49% were obtained from the questionnaire replies and the distributional information existent at the beginning of this study.

#### SALAMANDER SURVEYS

The selected streams were surveyed for salamander presence at least once during each field season. The method used to assess *E. platycephalus* presence in a particular site was a careful observation of the chosen stream-bed at different altitudes, and in pools scattered along the water course. Searches took from 3-6 hrs, not considering the time necessary to reach the site. Approximately 1 km of the water course was walked by a team of three/four people going upstream. In most cases, salamander presence was immediately confirmed as

TABLE 1. Text in English of the questionnaire distributed to forest stations in July 2000.

#### QUESTIONNAIRE ON EUPROCTUS PLATYCEPHALUS 2000

#### Forest Station:

Villages and Districts included:

- According to the field experience of Forestali personnel and their knowledge of territory and local fauna, is the species present in this area?
- · If yes, has it been observed recently?
- When (year and month)?
- Where (locality, stream, if possibile IGM coordinates)?
- If it has not been observed recently, was the species present in the past?
- When? When was its presence last assessed?
- What could be the reasons for decline or absence of the species in the area (water pollution, drought, anthropic presence, fishing, predators)?
- Other useful information (description of observed individuals, population density, personal notes).

		Minimum			Maximum		Mean		
	1999	2000	2001	1999	2000	2001	1999	2000	2001
Air temperature (°C)	20	16	13.5	28.5	30	27	23.4	25.7	23.6
Relative humidity (%)	48	45	40	79	85	75	63.9	59.4	55
Water temperature (°C)	12.5	11.7	12.7	24.5	24	21	17.9	17.2	16.2
Water pH	6.3	7	7	8.2	8.5	8.3	7	7.6	7.6
Water DO (mg/l)		6	3.4		10.6	12		8.1	7.7

TABLE 2. Environmental parameters collected during 1999, 2000 and 2001 field seasons in sites inhabited by *E. platycephalus*: minimum, maximum and mean values.

soon as the first pools inhabited by the species were reached (these animals tend to aggregate in parts of the stream). The observation of one individual was also considered a sign of the presence of a salamander population. The observation could take longer in the case of absence of the animals, because a longer tract of the stream was surveyed before ruling out the presence of salamanders. In this case, rocks and stones underwater were turned and the bottom of pools disturbed using a stick, in order to see if any individual were hiding in the substrate.

#### STREAM TYPES AND CHARACTERISTICS

In each inhabited survey site, some environmental parameters were collected (air and water temperature, relative humidity, water pH and dissolved oxygen, Table 2).

Most of these survey sites were mountain or hill streams flowing through the typical Mediterranean macchia covering most of the island. This landscape is dominated by scrub plants such as heather (Erica sp.), myrtle (Myrtus communis), juniper (Juniperus communis), olive (Olea europaea sylvestris), Cistus sp., and Pistacia lentiscus, as well as holm and cork oak forests (Quercus ilex and Q. suber). A few sites did not conform to this broad habitat type. The pool at S.Nicolò Gerrei is a concrete water store located in a field dominated by grasses and brambles (Rubus sp.). The artificial lake (Laghetto) located near Tempio, also has a slightly different vegetation structure as the area surrounding the lake has been cleared. Funtana Urpis, between Isili and Villanovatulo, is an artificial pool built along a watercourse. Pischina Urtaddala is a natural lake (already



FIG. 1. Vertical distribution of sites inhabited by *E. platycephalus*.

identified by Voesenek *et al.*, 1987) apparently isolated in a limestone locality, but it actually depends on the overflow of the Rio Flumineddu stream.

Streams and pools were completely open or canopycovered, or partially protected by overhanging rocks or vegetation. There was one exception, where a very interesting hypogeous *E. platycephalus* population was found living in a stream flowing inside a cave (Is Angurtidorgiu, near Perdasdefogu).

#### RESULTS

#### DISTRIBUTION OF E. PLATYCEPHALUS

Sardinian salamanders have a naturally patchy distribution across the island, showing association with small and temporary streams, pools and small lakes, ponds and springs, at a wide range of altitudes (from 100 to 1200 m) and with preference for sites between 400 and 800 m (Fig. 1). The species was found at sites with water temperature ranging between 11.7 and 24.5°C, water pH between 6.3 and 8.5, and water dissolved oxygen ranging from 3.4 to 12 mg/l (Table 2).

At the completion of this study, eight sites in the north, 18 in the centre and 18 in the south of Sardinia were identified as localities currently and/or recently (after 1991) inhabited by the species. A total of four sites in the north, four in the centre and three in the south, constituting 20% of all sites considered, have apparently lost the species in the last two decades (Table 3). For a detailed list of all the sites where the presence of the species has been assessed in the three years of research or within the last 10 years, see Table 4.

#### DISTRIBUTION IN WESTERN SARDINIA

The present distribution study focused particularly on the eastern part of Sardinia, where the presence of E. *platyce phalus* has always been confirmed in the past (Alcher, 1975; Puddu *et al.*, 1988) and which comprises the preferential habitat areas for these salamanders. The species is generally believed not to be present in most of the western areas, or its presence is questioned but not excluded (Alcher, 1975). There are very few records of observations on the west side of the island (forest station workers, pers. comm., Schenk *et al.*, 1995). Nevertheless, nine localities in the south-west of Sardinia (Table 5) have been visited at least twice over three years of re-

Locality	Mountain system	Year of observation	Source
Burcei (Rio Brabaisu)	Sette Fratelli	1990	Forest stnobs.
Muravera (Rio Picocca)	Sette Fratelli	1975	Amphibiaweb
Tertenia	Ogliastra	1985	Local comm.
Benetutti	Goceano	1990	Forest. stn. obs.
Bolotana	Marghine	1990	Local comm.
Alà dei Sardi	Monti di Alà	1974	Alcher (1975)
Siniscola	Monti di Alà	1974	Alcher (1975)
Nuoro	Gennargentu	1974	Alcher (1975)
Orgosolo	Gennargentu	1974	Alcher (1975)
Arzana	Gennargentu	1974	Alcher (1975)
Gairo	Ogliastra	1974	Alcher (1975)

TABLE 3. List of localities where *E. platycephalus* was present before 1991 (but where its presence was not confirmed more recently on the basis of the forestali station questionnaire) and source of information.

search. Salamanders were never observed. Fish presence (Salmo trutta) was recorded in four sites.

Combining past information and the results of the present distribution study, salamander presence in the south-west of the island cannot be completely ruled out. Undoubtedly, in these areas *E. platycephalus* is very rare, and possibly (considering comments and observations by Forestali workers and collaborators) in decline. Another mountainous area located in the north-west of the island, Marghine-Goceano, can also not be ruled out from the salamanders' range, as it has not been covered by this distribution survey. Few records exist on the past presence of the species (Schenk *et al.*, 1995).

#### FOREST STATION QUESTIONNAIRE

Responses on the presence/absence of the species were received from 60 of the 79 forest stations. Forty responses were negative, and 20 were positive. The negative responses contained some reports of the presence of the species in the past but not recently. The positive responses included photographs of salamanders, of study sites, and IGM (Istituto Geografico Militare) maps with the actual site where the species was seen indicated. Fig. 2 shows the distribution across Sardinia of the 60 Forestali districts that responded.

#### DISTRIBUTION MAPS

The general map (Fig. 3) shows the area where the species is present, combining historical and present data. Fig. 4 shows all the localities where species presence has been assessed during the three years of research and in the recent past (since 1991). The sites where it was known to be in the past (before 1991) but where it is no longer present (or at least can no longer be found) are also indicated. This map represents a first attempt to rectify the lack of field-based information on E. platycephalus distribution. It therefore provides a framework for further research on Sardinian salamander conservation.

## DISCUSSION

Through a combination of field and questionnaire surveys, conducted between 1999 and 2001, we have attempted to collate information on the present distribution of the endangered endemic Sardinian brook salamander, *E. platycephalus*. As mentioned in the Results section, a total of 14 localities where Sardinian salamanders are present today have been identified, as well as numerous sites where species presence has been recorded since 1991. A number of historical sites appear no longer inhabited by the species and these should receive particular concern. Conservation efforts should focus on further detailed surveys and habitat protection of salamander-inhabited areas.



FIG. 2. Distribution in Sardinia of forestry districts (Uffici Forestali) which replied to the *Euproctus platycephalus* questionnaire in 2000.

TABLE 4. List of sites where *E. platycephalus* presence was confirmed by the authors between 1999 and 2001 (top), and (bottom): by forestry workers or local collaborators (Source) after 1991. Italics indicate sites visited by the authors in 2001 where newt presence was not confirmed on the day of survey.

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i.			
Site	Mountain	Year of	Notes
	system	observation	
Rio S. Mannu	Sette Fratelli	1999	One individual
Rio Pressiu	Sette Fratelli	1999	One individual
Rio Gattu	Sette Fratelli	1999, 2000, 2001	High density
Rio Guventu	Sette Fratelli	2000, 2001	High density
Rio Melliana	Sette Fratelli	2000, 2001	Adults and larvae
Rio Angiulus	Sette Fratelli	2000,2001	Adults and larvae
Rio Su Zurru	Gerrei	2000, 2001	Adults and larvae
Is Angurtidorgiu	Quirra	2000, 2001	Hypogeous pop.
Roa Paolinu	Gennargentu	1999, 2000, 2001	High but declin.dens.
Rio Lardai	Gennargentu	2000, 2001	Adults and larvae
Funtana Urpis	Gennargentu	2000, 2001	One individual
Pischina	Supramonte	1999, 2000, 2001	High density
Rio Pisciaroni	Limbara	1999, 2000, 2001	High density
Loc. Letto di Fica	Gallura	1999	One larva
Site	Manutalia	V£	0
Site	Mountain	Year of	Source
	system	observation	
Rio Acquacallenti	Sette Fratelli	1999	Forestali Q.
Rio Baccusafigu	Sette Fratelli	1999	Forestali Q.
Rio Staulu Mannu	Sette Fratelli	1999	Forestali Q.
Rio Pireddu	Parteolla-Gerrei	1998	Forestali Q.
Rio Baccu Onnai	Quirra	1999	Forestali Q.
Rio Semida	Quirra	1999	Forestali Q.
Rio Piras	Quirra	1993	Forestali Q.
Rio Bauporcus	Marganai	1998	Forestali Q.
Rio Maurreddu	Sulcis	1995	Forestali Q.
Rio di Pula	Sulcis	1999	Local comm.
Rio Ermolinus	Gennargentu	1994	Forestali Q.
Rio S.Girolamo	Gennargentu	1994	Forestali O
Rio Longufresu	Gennargentu	1994	Forestali O.
Rio Samunudolgiu	Gennargentu	1999	<b>Forestali</b> O
Rio Pitzirimasa	Gennargentu	1999	Forestali O.
Rio Panargia	Gennargentu	1997	Forestali O.
Rio Conca Sarui	Gennargentu	2000	Forestali O.
Rio Mannu	Gennargentu	1995	Forestali O.
Rio Araxisi	Gennargentu	1995	Forestali O
Rio Flumineddu	Gennargentu	1994	Forestali O.
Rio Nesula	Gennargentu	1994	Forestali O.
Loc. Oliena	Gennargentu	1992	Forestali O.
Rio Tedderì	Gennargentu	1996	Forestali O.
Su cunn'es'ebba	Supramonte	1995	Local comm.
Salto di Giosso	Monti di Alà	1998	Forestali O.
Sorg. Caltaroni	Limbara	2000	Forestali O.
Rio Lo Frassu	Limbara	1999	Forestali O.
	Limbara	2000	Forestali ()
Laghetto		2000	
Laghetto Rio Sa Mela	Limbara	1995	Local comm

Site	Locality	Year of	Number of	E. platycephalus	Fish
		survey	surveys	presence	presence
		1000		0	
Rio Leni	Villacidro	1999	4	0	1
Rio Biddascema	Villacidro	1999	2	0	1
Sa spendula	Gonnosfanadiga	1999	2	0	0
Rio Bauporcus	Fluminimaggiore	2001	2	0	0
Rio Camboni	Uta	1999	2	0	1
Rio Guttureddu	Monte Arcosu	1999	3	0	0
Rio Gutturumannu	Santadi	2001	2	0	0
Rio AntoniPolla	Domus de Maria	2001	2	0	0
Rio Maurreddu	Pula	2001	2	0	1

TABLE 5. List of south-west sites surveyed by the authors (fieldwork seasons 1999-2001) for *E. platycephalus* distribution. Species presence, 1; absence, 0.

#### SURVEY METHODS

As discussed by Beebee (1996), species distributions are usually assessed by field survey, and this procedure is subject to possible errors such as misidentification and recorder bias. Moreover, stream amphibians are challenging to sample because they are unevenly distributed, cryptically coloured, and often hidden in the substrate (Welsh *et al.*, 1997). On the other hand, as many species have low dispersal abilities, in amphibian



FIG. 3. Grey area: general historical distribution of *E. platycephalus* in Sardinia.

surveys the observation of a single individual usually means a population is present nearby (Beebee, 1996).

Using local people's knowledge of sites has proved to be the best strategy to locate streams inhabited by



FIG. 4. Current distribution of *E. platycephalus* in Sardinia. Black spots: sites with *E. platycephalus* presence assessed, during 1999, 2000 and 2001 field work seasons (see Table 4). Grey spots: sites with species presence assessed (by forest station workers or local collaborators), after 1991 (see Table 4). White spots: sites with presence assessed in the past (before 1991), but not confirmed in the present, where the species could be locally extinct or have strongly declined (see Table 3).

salamander populations. Many of these are remote places, sometimes reachable only by knowing the territory very well and following concealed pathways through the Mediterranean macchia. Looking into pools and sections of a watercourse downstream – or relatively close to access paths or roads – is unlikely to reveal their presence as salamander populations often inhabit undisturbed parts of the watercourse. Only local fishermen or hunters sometimes visit these places. Some of the streams surveyed had long stretches that were dry during the summer months, so it was necessary to walk upstream for a while in order to find water (Rio Gattu, Rio Angiulus, Rio Mela).

Assessment of salamander presence was easier in the summer, when streams were drying up and isolated pools forming. Some sites where E. platycephalus was known to be present from previous observations did not give any clear information if visited too early in the season (April/early May), as the rapidly-flowing water did not permit the observation of salamanders in the stream. Salamanders are known to hibernate during the winter and sometimes aestivate in the summer (Puddu et al., 1988). The difficult observation of individuals in very early spring in some sites could also be due to the fact that the animals were not actually active in the water before a certain time of the year. In some places, though, it was possible to observe a great number of animals active throughout the year (Pischina Urtaddala, pers. comm.).

Assessing the presence or absence of animals in a particular site was usually straightforward. In many streams, after the first salamander was observed, it was easy to spot tens of others, either in the same or in neighbouring pools. In some streams, both larvae and adults were observed (Rio Lardai, Rio Melliana, Rio Su Zurru). A few sites had just a few or even one individual, and the presence of other specimens was impossible to confirm because of the particular characteristics of the study site (Funtana Urpis, an isolated artificial pool connected to a stream by underground water). The population inhabiting the Roa Paolinu stream (Gennargentu) appeared to decline in numbers over the three years. This could be due to a natural population fluctuation, or it could indicate that salamanders are declining in that area.

#### LITERATURE REVIEW

General and vague reviews of the mountainous range where salamanders occur are numerous, but very few field-based distribution studies exist on this endemic species.

In 1975, Alcher published a valuable attempt at mapping the distribution of *E. platycephalus*. Survey sites were described in terms of locality (the name of the closest village) and altitude, and cover eastern Sardinia, which was extensively visited over two summers (1973, 1974). It would be useful to repeat Alcher's survey today and obtain important information on the possible range contraction of the species. A detailed localization of the survey sites, with locality, altitude but especially exact geographic position and name of the stream where larvae or adults were observed would be necessary. The lack of this information has prevented the use of this almost unique distribution study in a more extensive and quantitative way. Only six areas indicated by Alcher (1975) as inhabited by the species in the 1970s, but where salamanders are no longer present (on the basis of forest station questionnaire replies and communications), were included in the distribution survey (see Table 3).

#### DISTRIBUTION MAPS

As shown in Fig. 4, sites in black and grey are all considered recently inhabited by *E. platycephalus*. Black refers to the assessment of species presence through our field surveys (conducted between 1999 and 2001), and grey through the questionnaire survey and local communications (presence recorded after 1991).

Black sites can be considered confirmed inhabited locations, where salamander populations have been repeatedly observed over the last three years (Table 4, upper part). Grey sites are locations where *E. platycephalus* was found in the last 10 years, but its presence is not documented or unconfirmed today (Table 4, lower part). At a number of grey sites (14), indicated by Forestali collaborators and visited during the 2001 fieldwork season, salamanders were absent from the pools surveyed on the day of sampling (sites in italics in the lower part of Table 4).

As shown in Fig. 2, the distribution of forest stations (districts) which replied to the *E. platycephalus* questionnaire is widespread and uniform over Sardinia. On average, the questionnaire survey provided a good coverage of the island, based on reliable observations of forestry workers over the years (a number of replies were accompanied by photos, map details and oral communications ruling out false positive cases).

Some of the black sites, such as Letto di Fica (Gallura), Rio Suergiu Mannu and Rio Pressiu (Sette Fratelli), where – during the three years – only one individual was observed, are also considered sites inhabited by the species. The lack of information on the habitat use and metapopulation structure of Sardinian salamanders prevent us from excluding sites from the distribution maps solely on the basis of the number of individuals observed. Besides, in amphibian surveys, finding a specimen normally means that a population exists in the immediate vicinity (Beebee, 1996).

Particularly important from a conservation point of view are the pools where a high number of individuals have been always observed in each of the distribution surveys (1999, 2000 and 2001), such as Rio Gattu (Sette Fratelli), Pischina Urtaddala (Supramonte) and Rio Pisciaroni (Limbara). These sites, together with the streams and ecosystems associated, should be particularly protected and the areas managed in order to minimize factors that could be detrimental to salamander population viability.

#### LOCAL DECLINES

White sites in the distribution map indicate historical localities where salamander populations were observed before 1991, but species presence was not recorded after that time (see Table 3). They are therefore considered sites where the species is undergoing local extinctions or declines. However, these results should be taken cautiously and a long-term detailed field investigation should be conducted before considering the species extinct from an area. In particular, the area around Alà and Nuoro should be monitored more carefully, as well as the areas of Berchidda, Benetutti and Bitti, indicated as no longer inhabited by E. platycephalus (forest station questionnaires). The whole Ogliastra and the mountains around Tertenia, Lanusei and Gairo, should also be carefully monitored, although a strong decline in salamander presence is implicated by the data. Special concern should be given to the western areas of the island, Monte Linas and Sulcis in the south, and Marghine-Goceano in the north, where species presence or absence needs to be confirmed and updated.

#### AMPHIBIAN DECLINE

Comparing the present results with previous data (Alcher, 1975) suggests that the distribution of the species has changed little. However, the population sizes of E. platycephalus seem to have declined in the past few decades (Puddu et al., 1988; Colomo, 1999; Rimpp & Thiesmeier, 1999), although this is not yet documented by an ecological census. Evidence could be found in some of the questionnaire replies, which report the presence of the species in a particular area in the past, but not today. This trend seems consistent with the global pattern of declining amphibian populations which was first described in 1990 (Blaustein & Wake, 1990) and then repeatedly documented over the last decade (Wake, 1998; Houlahan et al., 2000). Simultaneous and widespread reported declines are causing concern especially because they often occur in pristine and apparently intact areas. Some population declines can be realistically evaluated by comparing the present species distribution with historical data. Unfortunately, many endangered and threatened amphibians have not been extensively studied and monitored, and still lack high-resolution distribution maps or informative atlases. Research is needed on the most recent historical aspects of amphibian distributions, as there might have been considerable fine-scale changes over relatively short time spans (Beebee, 1996). Especially endangered or declining species should be monitored and atlases with the present distribution of populations produced.

#### IMPLICATIONS FOR CONSERVATION

Many sites indicated in the distribution maps witness the disappearance of the Sardinian brook salamander from parts of its previous range. However, there are a number of streams and localities spread in the north,

centre and south of the island where the species is represented by stable and apparently abundant populations (Rio Pisciaroni in the north; Rio Lardai and Pischina Urtaddala in the centre; Rio Guventu, Rio Gattu, Rio Melliana, Rio Angiulus, Rio Su Zurru and Is Angurtidorgiu in the south). The conservation of E. *platycephalus* should focus on these sites. Populations should be constantly monitored and further investigation should estimate population size and abundance. Associated habitats should be protected in order to keep the conditions that meet the ecological requirements of the species. Most of these streams flow through mountains and areas already designated as protected (Ente Foreste, Parchi Regionali). Nevertheless, the implementation of real conservation measures (such as fishing and tourism control), which would benefit not only endemic amphibians, but also many other organisms linked to the salamander habitat, has yet to be seen.

Some priorities for amphibian conservation and research in Sardinia are given here. The dissemination of information on E. platycephalus (and other endemic species) conservation status and distribution, and the creation (or implementation) of bioreserves and protected areas around the main stream and river systems are recommended. Freshwater ecosystems falling within the salamander's range should be given particular attention with respect to both study and conservation. Water pollution, expanding tourism and illegal fishing methods should be controlled, fish introduction stopped and possibly the removal of predatory fish from streams where they were not historically present attempted. A co-ordinated monitoring network (ideally with the aid of Forestali and Sardinian scientific institutions) for the island's whole herpetofauna should be created. This study provides the basis for future research on distribution changes, population expansions and declines of the endangered endemic Sardinian brook salamander. The most valuable application of these distribution data would be the improved management and conservation of the stream-related habitat in the Sardinian mountains and of the unique associated biodiversity.

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## LEATHERBACK TURTLES (DERMOCHELYS CORIACEA) IN ITALY AND IN THE MEDITERRANEAN BASIN

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A total of 411 records of leatherback turtles (*Dermochelys coriacea*) are reviewed for the whole of the Mediterranean, of which 57 are new records reported from Italy. Data on anthropogenic factors, spatio-temporal distribution, size and maturity are discussed. Leatherback turtles are most frequently captured incidentally by fishing nets. Specimens seem to concentrated in specific areas rather than being evenly distributed along a linear gradient from the Atlantic. Moreover, they frequent the Mediterranean all the year round without clear seasonal patterns of immigration or emigration. However, seasonal movements may occur between northern and southern coasts. Specimens entering the Mediterranean are likely to be large juveniles and adults of both sexes.

Key words: body size, by-catch, conservation, distribution, marine turtle, threats

#### INTRODUCTION

The leatherback sea turtle, *Dermochelys coriacea* (Vandelli, 1761) is in danger of extinction because of human impacts affecting its populations worldwide (Spotila *et al.*, 1996) and is listed as Critically Endangered in the IUCN Red List of Threatened Species (Hilton-Taylor, 2000). It has the widest range among sea turtles (and even among reptiles), occurring at high latitudes (Marquez, 1990) thanks to its thermoregulatory capability (Paladino *et al.*, 1990). It is the most pelagic turtle and seems to feed mainly upon jellyfish and other pelagic invertebrates (Bjorndal, 1997). Specimens frequent the Mediterranean, but they are likely to originate in the Atlantic, since reproduction in the Mediterranean, if it occurs, is certainly exceptional (Lescure *et al.*, 1989).

Unfortunately, the presence of this species in the Mediterranean is often known only from anecdotal information, and just a few individual records exist. Moreover, reliable data are usually dispersed between different journals, and only a few authors have reviewed data from a Mediterranean perspective (Capra, 1949; Capocaccia, 1968; Delaugerre, 1987; 31, 55, and 109 records respectively.

The aim of this study is to report data obtained from a large sample of individual records, in order to provide information on the distribution and threats to this species in the Mediterranean. Some of the Italian records have appeared in congress presentations (Nicolosi *et al.*, 2001; Casale *et al.*, in press).

#### MATERIALS AND METHODS

Information about leatherback turtles found in Italy was collected from individual reports to authorities, scientists or newspapers, mainly in the framework of a tagging and awareness programme carried out between 1981 and 2000 (Argano, 1992). Some of these records eventually appeared in articles by participants in the program, and are reported here as reviewed records. Moreover, a form was distributed to Italian museums in order to gather information about leatherback turtles held in their collections, and any other records as well. Finally, published Italian and Mediterranean records dispersed through different kinds of international and national journals were collected by means of a bibliographic search (which, though accurate, certainly cannot be considered complete), and by using previous reviews and the bibliographic synthesis by Laurent (1998). As several articles made partial reviews, each record was compared with others in order to avoid duplication.

Specimens were classified as follows: captured incidentally during fishing operations, taken from the sea surface by hand, stranded, and sighted. Captures during fishing operations were classified as follows: longline, set and drifting nets, unspecified nets (most are likely to be set or drift nets, because different names are usually used for trawl nets), trawl, other and unknown fishing equipment. When available, lengths of specimens where classified as follows: unspecified length, total length (TL), unspecified carapace length (CL), curved carapace length (CCL), and straight carapace length (SCL). It should be taken into account that unspecified carapace lengths are likely to be curved measures, as this is the easiest to obtain, and that total lengths may not be com-

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FIG. 1. Geographical distribution of Mediterranean records (n=411). Small circles: single records; large circles: 13 (Straits of Gibraltar), 25 (Spain), 19 (Pelagian Islands, Italy), 13 (Malta), 14 (Straits of Messina), 14 (Gulf of Taranto) records. Dotted lines: arbitrary divisions between western and eastern basins, and between northern and southern Mediterranean coasts.

parable, as they can be obtained in different ways: straight, ventral side, or dorsal side.

#### **RESULTS AND DISCUSSION**

We collected a total of 411 individual records for the whole of the Mediterranean (Fig. 1) with 152 of these from Italy, of which 57 are reported in the present work for the first time. Records concerned turtles stranded (n=52), taken (n=9), captured (n=170), sighted (n=53), or found in unknown circumstances (n=127). A listing of all records is available as an electronic supplement on the *Herpetological Journal* website: http://biology.bangor.ac.uk/~bss166/HJ/

#### ANTHROPOGENIC IMPACTS

Specimens reported by fishermen (n=170) were caught by set or drift nets (29.4%), longlines (20.6%), unspecified nets (12.9%), trawl (4.7%), other fishing equipment (9.4%), and unknown fishing equipment (22.9%). Proportions of specimens caught by different fishing equipment are particularly interesting, because finding a leatherback turtle is an exceptional event that is usually reported, and so this should theoretically give a realistic picture of the interaction between turtles and fishing activities. Moreover, the turtle project operating in Italy since 1981 focused particularly on longline fishing and so, if a bias exists, it should be towards this method. Thus, on the basis of present results it is likely that set/drift nets and unspecified nets (which are likely to be set or drift nets too) are responsible of most of the incidental catch of this species, as the majority (55%) of specimens caught by known equipment were caught by these methods.

Out of the 17 specimens caught in Italy by longline, three were dead, and four alive, while the final condition of the other 10 was unknown. The deaths of two specimens could be due to causes other than the fishing equipment, while one specimen died as a result of the damage caused by internal hooks. This is an uncommon event: the great majority of leatherback turtles caught by longline are found entangled in the branch-line or hooked externally (e.g. Witzell & Cramer, 1995).

Of the specimens caught in Italy by set/drift nets (n=13) and unspecified nets (n=19), 23.1% and at least 52.6% (the status of two specimens is unknown) died respectively. Proportions for the whole of the Mediterranean are at least 36.0% (n=50); the status of 11 specimens is unknown) and at least 54.5% (n=22); the status of two specimens is unknown), respectively. Hence, present data suggest that incidental capture of turtles as part of fishing activities causes high mortality and represents a significant threat.

Among the 20 specimens stranded in Italy (most died: only one was released alive), five had injuries on the head and/or carapace, presumably due to impacts with boats or their propellers; at least three had been caught by set/drift nets, and at least one had plastic bags in the digestive tract.

#### SPATIO-TEMPORAL DISTRIBUTION

Arbitrarily dividing the Mediterranean into two subareas at Cape Bon (Tunisia) - Sicily (Italy) (Fig. 1), Italian records were equally distributed between the eastern (74: 56 in the Ionian/Sicily Channel and 18 in the Adriatic Sea) and the western (75: Tyrrhenian Sea) Mediterranean side, but some possible methodological biases due to different efforts in collecting information should be taken into account. In order to reduce such possible biases two considerations may help. First, the number of specimens reported by fishermen is likely to depend on research effort rather than the number of those stranded, gathered, or sighted. Second, the geographical distribution of specimens caught by nets are likely to be relatively unbiased, because these fishing

Area	Turtles	Hooks	Days	Turtles/ 1000 hooks	Turtles/ day	Source
Spain	2	1 572 965	792	0.0013	0.0025	Camiñas & Valeiras, 2001
Italy, Tyrrhenian	1	19 610	24	0.0510	0.0417	Guglielmi et al., 2000
Italy, Sicilian Channel	2	109 375	114	0.0183	0.0175	Guglielmi et al., 2000
Italy, Western Ionian	0	13 974	37	0.0000	0.0000	Guglielmi et al., 2000
Italy, Northern Ionian	4	1 513 481	1935	0.0026	0.0021	De Metrio et al., 1983
Italy, Western and						
Northern Ionian	0	437 500	318	0.0000	0.0000	De Metrio & Deflorio, 2001
Greece, Eastern Ionian	0	_	785	-	0.0000	Panou et al., 1999
Greece, East						
Ionian and Aegean	1	320 209	255	0.0031	0.0039	Kapantagakis, 2001

TABLE 1. Number of *Dermochelys coriacea* specimens caught by drifting longlines intended for swordfish during studies carried out in different Mediterranean areas, with fishing effort in number of hooks and days, and the corresponding catch rates.

activities were not associated with awareness campaigns as others were. So, taking into account only specimens caught by nets, most (84.4%; n=32) were caught on the western side (Tyrrhenian). Although it cannot be excluded that this difference is due to different fishing efforts, this pattern conforms to a strong west-east gradient with most records in the western basin explained by the Atlantic origin of the specimens (e.g. Capocaccia, 1968: Oliver. 1986; Duron-Dufrenne, 1986: Delaugerre, 1987). However, it is possible that the observed Mediterranean distribution is partially biased by differences in research effort in different areas. Indeed, in the present review the apparently skewed distribution of Mediterranean records (239 and 169 records in the western and eastern basin respectively) is due to records from Spain and France. These are countries where research interest in this species and the amount of reporting might have been higher than in countries in the eastern basin. No skewed distribution is evident if only the southern Mediterranean coast (Gibraltar Strait to Israel, including the Spanish territories in north Africa) is considered: even including the 11 records from "Gibraltar Strait" as southern, 52 and 50 records were from the western and eastern basin respectively. Recent investigations from the eastern Mediterranean (Margaritoulis, 1986; Camiñas, 1998; Taskavak & Farkas, 1998) seem to suggest that with a greater research effort many more records could come from areas under-represented at the moment. It is interesting that western Mediterranean records decreased from the 69.8% of Capocaccia's (1968) review to 58.6% of the present one (n=408: the exact position of three records in Italy was unknown).

Certainly, caution is needed when comparison is made of countries where research effort may vary. A rigorous comparison could only be made by using a standardized approach. Catch rates by different fishing activities could be useful, but such data are unfortunately limited. Even though based on a limited sample size, catch rates of longline fishing targeted at swordfish (Table 1) represent the best standardization available at present. Assuming that the catch effort is proportional to the number of hooks/branch-lines (leatherback turtles are usually entangled in branch-lines or hooked; e.g. Witzell & Cramer, 1995) such a comparison does not suggest any west-east gradient; actually, both catch rates from Italy/Tyrrhenian and Italy/Sicily Channel are higher than the one from Spain (Fisher exact test, P < 0.05, n=1 592 575 and n=1 682 340 respectively). Margaritoulis (1986) reported that most Greek records were from the Aegean Sea (it is interesting that the only specimen reported from Greece in Table 1 was also from the Aegean) and that while leatherback turtles were well known by fishermen of this area, it was not so for fishermen from other areas, suggesting a gradient opposite to that (west-east) in Greek waters. In conclusion, even though at present most records are from the western basin and leatherbacks seem to occur more on the western



FIG. 2. Temporal distribution in the western and eastern basins (n=310).



FIG. 3. Temporal distribution in the northern and southern coasts (n=310).

side of Italy, there is no strong evidence of a west-east gradient at Mediterranean level; it is certainly possible that the distance from the Atlantic is only one of the factors determining the distribution of this highly vagile species in the Mediterranean, and that specimens might concentrate in particular areas (for instance, in the Tyrrhenian and Aegean Seas), probably for feeding reasons.

Seasonally, records are concentrated in the warmperiod of the year (Fig. 2), but it is possible that such a distribution reflects that of the human activities responsible for the findings, rather than the actual temporal distribution of the species. Seasonal differences between western and eastern basins do not seem to occur (Fig. 2;  $\chi^2$ =8.91, df=3, P>0.05, n=310), suggesting the lack of strong seasonal movements between them. Since it is assumed that specimens originate in the Atlantic, this also suggests that the species is present in the Mediterranean all the year round, without an evident seasonal immigration/emigration pattern. Conversely, turtles seem to move northwards in summer (Fig. 3;  $\chi^2$ =38.02, df=3, P < 0.0001, n=310), although biases due to seasonal differences in research and fishing effort or reporting rate cannot be completely excluded.

#### SIZE AND SEX

Known carapace lengths (curved and unspecified, excluding one specimen of 6.6 cm; Lescure *et al.*, 1989) ranged between 112 and 190 cm (mean=145.0, SD= 17.2, n=83; Fig. 4). Curved-line carapace lengths ranged between 115 and 190 cm (mean=145.5, SD=16.4, n=44; Fig. 4). In two important Atlantic nesting grounds, French Guyana and the Virgin Islands, the mean CCLs of observed nesting females were 157.4 cm (n=192) and 153.6 cm (n=39) (van Buskirk & Crowder, 1994); in the latter place, about 90% of specimens were larger than 144 cm CCL (n=358; Boulon *et al.*, 1996). NMFS (2001) and Eckert (2002) considered as juvenile those specimens less than 145 cm CCL.

Twenty-eight specimens were reported to be female (14 through direct observation of ovaries or specifically of large follicles/eggs, another also through necropsy, but without specific indications, and 13 through an unknown method) and 16 were reported to be male (an immature determined through direct observation of pe-





nis, and 15 through unknown methods - but probably at least some of them assigned using presence of the elongated tail typical of mature males). Those females with known carapace length for which the authors reported the presence of ovaries were 115 CCL, 130 CL, 145 CCL cm long and those for which the authors specifically reported only the presence of large follicles/eggs were 130 CL, 132 CCL, 150 CL, 155 CCL, 158 CCL, 190 CL cm. The immature male had a CCL of 136 cm (Turkey). All these data on size and internal anatomy suggest that the Mediterranean is frequented by both adults (certainly females and probably also males) and large juveniles (both sexes). It is interesting that - except for one very small specimen - small juveniles have never been reported, suggesting that neither the Mediterranean nor the north-east Atlantic are areas where the Atlantic populations of this species spend time as small juveniles. This is consistent with size data from the north-west Atlantic (NMFS, 2001), and suggests that small juveniles are limited to lower latitudes in the north Atlantic. Accordingly, a recent analysis based on the distribution of 98 small (<145 cm CCL) specimens around the world suggests that leatherbacks do not leave tropical waters before reaching a size of about 100 cm, probably because of thermal constraints (Eckert, 2002).

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#### AN ETHOGRAM FOR ADULT MALE RAINBOW SKINKS, CARLIA JARNOLDAE

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An ethogram for male rainbow skinks, Carlia jarnoldae (mean snout-to-vent length 44 mm), was derived from observations of captive individuals in large, semi-natural field enclosures during the summer. Males were observed in one of four treatments: solitary, socially with a male conspecific, socially with a female conspecific, or with a model of an avian predator. We identified 32 different types of behaviour, including postures and simple movements. Six of the behaviours (dorsolateral orientation, head bob, letisimulation, slow motion, throat flash and tail wave) are of particular interest because their functions are either controversial or unknown. We describe them in detail, and infer their functional significance from the contexts in which they occurred. Dorsolateral orientation and slow motion behaviours appear to function primarily in courtship; throat flashes may provide information to conspecifics; and letisimulation may function as an antipredator behaviour. The function of head bobs remains unresolved, and tail waves appear to signal residency, but need further investigation. Although the behaviours exhibited by C. jarnoldae males were generally similar to those reported in other skinks, two of the behaviours we observed (letisimulation and throat flash) have not previously been recorded in a skink. Carlia jarnoldae males were outside refugia for most of our observation periods, and appeared to defend areas of the enclosures from conspecific males. Both visual signals (dorsolateral orientations, slow-motion behaviour and throat flashes) and chemical cues were used to communicate with conspecifics.

Key words: behaviour, lizard, social interactions, visual signals

#### INTRODUCTION

Lizards provide an excellent model system for studying signal evolution. However, the scientific literature on lizard social behaviour displays a strong taxonomic bias, with disproportionate attention to certain lineages, such as iguanids (Carpenter & Ferguson, 1977; Stamps, 1977; Ord et al., 2001). Although the family Scincidae is one of the largest and most diverse lizard lineages (ecologically, geographically and morphologically), the social behaviour of scincids has received far less attention than many other groups. Small skinks are thought to lack obvious social displays (Done & Heatwole, 1977; Stamps, 1977), but recent research has revealed that skinks exhibit complex social characteristics, including stable social aggregations (Greer, 1989; Gardner et al., 2001), kin recognition (Bull, 2000; Bull et al., 2000, 2001), female mate choice (Cooper & Vitt, 1993), mate guarding (Olsson & Shine, 1998), and aggressive territory defence (Jennings & Thompson, 1999).

Skinks occur virtually worldwide, but are most diverse in Australia (>300 species: Cogger, 2000). Nevertheless, we have been able to locate in the literature comprehensive descriptions of behavioural repertoires (ethograms) for only three species of Australian skink (*Carlia rostralis*: Whittier & Martin, 1992; Whittier, 1994; *Lampropholis guichenoti*: Torr & Shine, 1994; *Ctenotus fallens*: Jennings & Thompson, 1999), as well as for one North American species (*Eumeces inexpectatus*: Perrill, 1980). Before we can

understand and interpret the evolution of behavioural traits in lizards, we need to document patterns in a large number of phylogenetically divergent lineages. Ethograms for a range of species are necessary before we can undertake comparative studies.

This study aims to provide a thorough account of the behaviours displayed by males of an Australian skink, *Carlia jarnoldae*, under a range of circumstances, and to explore their probable function. We observed males in naturalistic outdoor enclosures in one of four treatments: while alone, with a female conspecific, with a male conspecific, or in the presence of a "predator". We describe the behaviours observed during these trials, and discuss the functional significance of various behaviours by examining the degree to which they are performed in the different treatments.

#### METHODS

Carlia jarnoldae is a diurnal skink found throughout north-eastern Queensland (Cogger, 2000). It is locally abundant in the Townsville region, inhabiting rocky areas in dry sclerophyll forest and tropical woodlands. It is a small skink – adult males average 44 mm snout-vent length (SVL), 68 mm tail length and weigh 2.4 g; adult females average 43 mm SVL, 64 mm tail length and weigh 1.9 g. Adults show striking sexual dimorphism; males are heavier, but not longer, and much more colourful than are females (Cogger, 2000).

The behaviour of males was observed over two summers (January to March), in 1999 and 2001. This season falls within the normal mating period of this species, which is from October to June (pers. obs.). We collected 66 individuals (11 females and 55 males) from Campus

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Creek, James Cook University, Townsville, Australia (19º 16'S, 146º 48'E). These skinks are capable of tail autotomy and - because tail loss may alter an animal's behaviour - we used only animals with complete tails. We randomly designated individual males as either focal (n=44) or stimulus (n=11) animals, while females were all used as stimulus animals (n=11). Focal males were observed and their behaviour was recorded during observation periods, and stimulus animals were introduced into the enclosures of focal males during social observations. Both focal and stimulus individuals were marked on the top of the snout with a small  $(2 \times 2 \text{ mm})$ spot of coloured nail polish to facilitate visual identification from a distance. Focal and stimulus individuals were marked with different colours, which were assigned randomly. This mark did not influence the lizards' behaviour (Langkilde, 1999), as marks were relatively inconspicuous, and skink displays involving colour are generally oriented laterally (pers. obs.; Carpenter & Ferguson, 1977; Whittier, 1994).

For observations, skinks were housed separately in one of eight oval, plastic enclosures  $(200 \times 100 \times 50)$ cm,  $L \times W \times D$ ). These enclosures were located outdoors at JCU campus. The enclosures received direct natural sunlight from approximately 0700 hrs to 1830 hrs each day. Each enclosure was partially covered with shade cloth (patches of cloth shading 50% or 80% of incoming solar radiation were used), providing skinks with sunny and shady areas, similar to the wild, to allow natural basking behaviour (pers. obs.). Animals were visible for most of our observation periods. Water was available ad libitum, and individuals were able to feed on insects that frequently entered the open enclosures. There was no significant change in mass of skinks from the day of capture to the day of release (paired samples *t*-test: *t*= 0.459, df=24, *P*=0.65, 4-15 days; average 10.6 days) indicating that food supply was sufficient. Each enclosure contained sand and leaf litter as substrate, and two wooden boards (300  $\times$  200 mm, L  $\times$  W) that were slightly raised above the substrate at one end provided shelters, basking sites, and display areas. We randomly assigned skinks to the enclosures 24-48 hrs prior to behavioural observations.

The behaviour of male C. jarnoldae was observed in one of four treatments: focal animal alone ("solitary" observations; n=11), focal animal with a male conspecific ("social + male" observations; n=11), focal animal with a female conspecific ("social + female" observations; n=11), and focal animal exposed to a predator ("predator" observations; n=11). All observations were made from behind an opaque screen to minimize observer effects. During solitary observation periods we simply observed the focal animal. During social observation periods, a conspecific male or female was placed in the vicinity of the focal male. The observer then withdrew behind the blind, and waited 5 minutes before commencing observations. The introduced non-focal animal was removed 20 minutes later. No injuries resulted during aggressive interactions. During predator observation periods, we placed a taxidermic mount of a laughing kookaburra (*Dacelo novaeguineae*) on the rim of the enclosures. Kookaburras are visual predators of small lizards (Barker & Vestjens, 1989), and spend much of their time perched in trees watching for prey (Simpson *et al.*, 1996). Therefore, the model was arranged in a natural pose on the edge of the enclosure, providing a stimulus similar to that of a real bird. We observed the focal male for 20 minutes (commencing 5 minutes after withdrawing behind the blind), and then removed the kookaburra.

All observations were made between 0700 and 1100 hrs, corresponding to the period of maximum activity in the wild (pers. obs.). On each observation day, we determined the order in which individual focal males were to be observed with a random numbers table. Observation periods were always 20 minutes, commencing 5 minutes after withdrawing behind the blind. Within 5 minutes of withdrawing behind the blind, skinks had usually emerged from under the shelters to which they fled when approached. Observations were made using a customwritten event-recording program on an HP 200LX palmtop computer. At the completion of testing, visual identification marks were removed, all animals were individually marked by toe clipping to avoid recapture and they were released at the point of capture.

#### DATA ANALYSIS

Only animals that were fully visible (i.e. not hidden under the shelters) for at least five minutes of the observation period were used in the analyses, as it is not possible to observe and record all behaviours exhibited by partly emerged animals, and shorter periods of exposure were too brief to provide a reasonable sample of possible behaviours. Kruskal-Wallis tests were used to analyse the number of males that performed each behaviour. Analyses of the number of times each male performed each behaviour during the 20 minute observation period yielded quantitatively similar results.

#### RESULTS AND INTERPRETATION OF BEHAVIOURS

Thirty-two behaviours were observed in male *C. jarnoldae* (Table 1). Females were also observed during the "social + female" trials, but their behaviour was not recorded as it was impossible to record the behaviour of two individuals simultaneously. Thus, although we were unable to quantify female behaviours and determine their functional significance, we were able to verify that females displayed similar behaviours. Females were observed performing 23 of the 32 behaviours recorded. The only behaviours we did not observe in females were those associated with mating, fighting or displays in males, such as copulations and flank bites, fighting, and dorsolateral orientations. We also did not observe females gaping.

#### ETHOGRAM FOR RAINBOW SKINKS

TABLE 1. The following behaviours were recognized in captive male *C. jarnoldae*. These behaviours have been assigned to functional categories, based on the results of this and previous studies on lizard behaviour (Carpenter *et al.*, 1970; Done & Heatwole, 1977; Whittier & Martin, 1992; Torr & Shine, 1994; Whittier, 1994). For behaviours that were previously unknown, or for which the function was previously unresolved, we have justified the classification in more detail later (these are indicated with an \*). There are five behaviours which remain unresolved, as they are either rarely observed, or occur in all contexts.

Functional category	Behaviour	Description
Courtship	Dorsolateral orientation*	Slight dorsoventral compression of the body and postural adjustment so that the body is tilted and dorsolaterally presented to a stimulus
	Slow motion*	All movements occur in short, rapid jerks, appearing as if under a strobe light.
MATING	Cloaca drag	Pulling the body forward with the forelimbs while keeping the cloacal region in contact with the substrate.
	Copulation	Insertion of hemipenis and pelvic thrusting while cloacae are in opposition.
	Flank bite	Mouth grip by the male on the skin of the neck or side of the female, maintained during copulation.
	Pelvic thrust	Forward thrusting movements of the pelvic region and the base of the tail by the male during copulation.
Aggressive	Bite	One skink grasps another in its jaws.
	Fight	Vigorously encountering another individual, usually involving some
		contact and biting.
Social	Throat flash*	An exaggerated mouth scrape, resulting in complete exposure of the gular colouration in the direction of a stimulus.
Maintenance	Adpress	One or more limbs raised off the substrate and held against the side of the body.
	Bask flat	A conspicuous dorsoventral flattening of the body against the
	Deels bish	substrate (occurs both in the sun and in the shade).
	Bask nign	(occurs in both sun and shade)
	Bask raised	Head raised but forebody resting against the substrate (occurs in both sun and shade).
	Defecate	The tail is raised and the body moved forward as faeces are passed.
	Drink	The snout is placed in water or against dew and the tongue slowly protruded and returned to the mouth.
	Eat	A food item is grasped in the jaws and consumed.
	Forage	Movement through vegetation and under ground debris such as leaf
	Leglift	litter while turning head and tongue flicking.
	Leg III	Reduces contact with hot substrate.
	Mouth scrape	The side of the mouth is scraped on a hard substrate.
MOVEMENT	Crawl	A slow, forward movement with the body in contact with the substrate.
	Jump	Leap into the air such that all four feet leave the substrate.
	Run	A fast, forward movement with the body raised off the substrate.
Exploratory	Tongue flick	The rapid movement of the tongue in and out of the mouth.
	Turn head	Movement of the head while the body remains motionless. (Looking around).
Escape	Flee Patrol	One skink moves quickly away from another skink or a predator. Running or crawling along the perimeter of the enclosure.

Antipredator	Letisimulation*	Actions taken by an individual that convey the impression that the individual is dead. "Playing dead".
Unresolved	Arc tail	Raise the tail in an arc, with the distal portion brought forward over the back.
	Gape	A wide opening of the jaws.
	Head bob	Relatively rapid movement of the head up and down from the neck.
	Tail undulate*	A sinusoidal movement of the entire tail while the tail is held horizon- tally just above the substrate.
	Tail wave*	Movement of the tail in a waving motion, occurring at different levels of intensity.

TABLE 1. (continued...)

Males exhibited a wide range of social behaviours, and interacted socially with most individuals they encountered, although these interactions were generally brief (approximately 3-5 minutes). During "social + male" encounters, males were observed attacking other males, chasing them around the enclosures and occasionally biting them, and chasing them out from under the shelters. In one trial, we observed males fighting, and in five trials we observed males chasing each other. None of these behaviours were observed in any other treatment. Generally, the active period (lasting approximately 45 min) was spent basking (mean percentage time ±SE: 72.19±4.04 secs), interspersed with periods of inactivity during which refuge was sought (mean percentage time ±SE: 24.10±16.32 secs), and occasional periods of foraging behaviour (mean percentage time ±SE: 1.78;±0.61 secs).

The behaviour of individuals in enclosures was similar to that observed in the wild (Langkilde, 1999). The majority of the behaviours we observed were similar to those reported for other skinks (Carpenter & Ferguson, 1977; Torr & Shine, 1994; Whittier, 1994); however, a few have not been previously described, or their function is unclear because they have not been systematically observed under different controlled circumstances. Of these behaviours, we give a more detailed description of those that were commonly observed, and infer their probable significance from the contexts in which they are performed. The other unresolved behaviours (arc tail, gape and tail undulate) were observed too rarely to infer their function from our data.

#### DORSOLATERAL ORIENTATIONS

Dorsolateral orientations were performed by significantly more males (H=6.6, df=3, P<0.001) when a conspecific female was present (6/11 males) than in any other treatment (1/11 males in predator trial, and none in any other treatment). This behaviour was performed for an average of 10.6 (±2.93 SE) seconds.

Dorsolateral orientations are performed by dorsoventrally compressing the body and positioning it in such a way that it is dorsolaterally presented to a stimulus individual. This posture exaggerates the male's body size and profile, and exposes the dorsal series of black and white stripes, the lateral band of blue spots on a black background, and the bright orange lateral coloration of male *C. jarnoldae*.

Both lateral presenting and lateral tilting postures have been described as separate aggressive behaviours in many lizards, including skinks (Mount, 1963; Perrill, 1980; Cooper & Vitt, 1988; Torr & Shine, 1994; Jennings & Thompson, 1999), agamids (Carpenter et al., 1970; Brattstrom, 1971) and iguanids (Greenberg, 1977a, b), but their simultaneous use has only been described in one lizard species, the skink, C. rostralis (Whittier, 1994). C. rostralis males use this behaviour primarily in dominance/subordination interactions with other males (Whittier, 1994). The function of this behaviour may be similar in the two species: to make the animal appear larger and more colourful. C. rostralis appear to perform dorsolateral orientations to seem larger and more threatening to a rival male (Whittier, 1994), whereas C. jarnoldae may perform this display to "impress" females with their size and colour, or as a general signal of fitness to females (and possibly predators: Rohwer, 1982; Cooper & Greenberg, 1992).

#### Head Bob

Almost all males (41/44) were observed performing head bobs, and the proportion of males that performed this behaviour did not significantly differ between treatments (H=0.73, df=3, P=0.28). This behaviour lasts for an average of 1.48 (±0.32 SE) seconds.

Head bob behaviours have been observed in many lizards, including skinks (Done & Heatwole, 1977; Torr & Shine, 1994; Whittier, 1994), iguanids (Phillips, 1995; Jenssen *et al.*, 2000) and agamids (LeBas & Marshall, 2000; Znari & Benfaida, 2001). Head bobs performed by iguanids and agamids are complex and highly ritualized (Carpenter *et al.*, 1970; Lovern *et al.*, 1999; Jenssen *et al.*, 2000). *C. jarnoldae* performed headbobs at varying amplitudes and frequencies, but as each bob was extremely rapid it was not possible to record these variations. In other species (iguanids and agamids), this behaviour is a submissive social signal associated with territorial fighting and courtship, and

functions as a threat or challenge signal (Brattstrom, 1971; Greenberg, 1977*a*; Phillips, 1995). It may also increase visual acuity, possibly enhancing depth of field (e.g. as in *Chamaelinorops barbouri*: Jenssen & Feely, 1991, and possibly *Lampropholis guichenoti*: Torr & Shine, 1994).

*C. jarnoldae* perform head bobs in all contexts, even when solitary, thus they may have multiple functions. It would be interesting to determine whether head bobs are used to different extents by resident and non-resident animals.

#### LETISIMULATION

This is the first record of death-feigning behaviour in a skink. Both males (n=5) and females (n=7) exhibited letisimulation behaviour, but only in response to being captured by a human. Upon capture, the skink would convulse and its body and legs would become rigid. This would last until the skink was replaced on the ground or otherwise stimulated to move (e.g. by blowing on it), though if a letisimulating individual were gently placed upside down on a rock it would remain in this pose until stimulated to move. The skink would then quickly right itself and flee. Some individuals would repeat this behaviour each time they were captured, and flee each time they were released. Letisimulation behaviour may reduce predation risk, as movement is a cue used by predators to facilitate prey detection (Gluesing, 1983), so remaining motionless may cause predators to release prey or abandon pursuit.

#### SLOW MOTION

Slow motion behaviour was performed by significantly more males when a female was present (5/11 males; H=7.13, df =3, P=0.005), but was occasionally observed during "social + male" (2/11 males) and "predator" trials (1/11 males). This behaviour lasts for an average of 9.29 (±2.92 SE) seconds.

When performing slow motion, all movements appear short and jerky, as if being viewed under a strobe light. Slow motion has only been reported in a few species of lizard, and is thought to function as a courtship display in some (*Anguis fragilis*: Palmer, 1937; *Crotaphytus collaris*: Greenberg, 1945), and have an antipredator function in others (*Lacerta vivipara*: Thoen *et al.*, 1986; Van Damme *et al.*, 1990; and *Oedura lesueurii*: Downes & Adams, 2001). Torr & Shine (1994) suggested that slow motion in *Lampropholis guichenoti* may be an assertion display in agonistic interactions, and provided circumstantial evidence that a pheromone may be associated with this behaviour.

Slow motion is performed by male *C. jarnoldae* primarily in the presence of females and may play a part in courtship. It is difficult to say how it would function in courtship, but it is possible that it may appease the female, allowing the male to approach. Alternately it may act as an "honest" signal of strength and endurance, or control and co-ordination, as it is a vigorous behaviour that involves the use of many muscles in opposition to each other, and may be energetically costly. Slow motion behaviours are also directed at conspecific males, possibly as a threat display, and may act as an "honest" signal of superior escape ability in the presence of a predator (Leal & Rodriguez-Robles, 1995; Leal & Rodriguez-Robles, 1997*a*,*b*; Leal, 1999).

#### THROAT FLASH

The proportion of males that performed this behaviour differed significantly between treatments (H=9.33, df =3, P=0.005). Males mostly performed this behaviour during social trials (8/11 males for "social + female"trials, and 6/11 males for "social + male" trials), some during "predator" trials (4/11 males) and none during solitary trials. This behaviour lasts an average of 2.93 ( $\pm$  0.39 SE) seconds.

The gular coloration of adult C. jarnoldae males is pale bluish-white, which becomes brilliant blue during the reproductive season, whereas that of females and juveniles is white to grey. C. jarnoldae males display this gular coloration by turning the head laterally until the throat is facing the stimulus individual, and angling the head towards the substrate before sweeping the head back into its original position. This behaviour appears to be an exaggerated and ritualized form of the mouth scrape behaviour, which is apparently used to remove food from the sides of the mouth after eating. Throat flashes start from a higher position than do mouth scrapes, and with the head turned more and therefore displaying more of the throat. During a throat flash the head is moved in a horizontal arc rather than being scraped along the substrate, with the jaw barely touching the latter.

The gular region is displayed in behaviours performed by many lizards, such as dewlap extensions in iguanids (Zucker, 1994; Carpenter, 1995; Zucker & Murray, 1996; Tokarz, 2002), throat displays in agamids (Brattstrom, 1971; LeBas & Marshall, 2000) and varanids (Bels *et al.*, 1995), and the "head raised" posture in the skink *Carlia rostralis* (Whittier, 1994), but this is the first record of the throat being displayed when the head is turned to the side.

Gular coloration provides information about age and sex that can be assessed from a distance (Whittier, 1994; Carpenter, 1995), and can be used to signal dominant status and exhibit territorial behaviour (Zucker, 1994; Bels *et al.*, 1995; Tokarz, 2002). This display probably provides similar information in this species, as the throat coloration of C. *jarnoldae* is different in males, females and juveniles and becomes exaggerated during the mating season, and throat flash behaviour is performed mostly during social trials. This behaviour is also performed when a predator is present, indicating that it may also function as a signal to predators, though the intended message is unclear.

#### TAIL WAVES

Tail waves occurred at three intensities that appeared to be part of a continuum of waves with similar functions: at the lowest intensity, skinks waved the distal third of the tail from side to side; next they moved the whole tail from side to side, and at the highest intensity they vigorously lashed the whole tail along the side of the body and over the back. Tail waves were very commonly performed by males of this species, but were performed by significantly fewer males when alone (4/ 11 males) than in any other treatment (9/11 males for 'social + female' trials; 9/11 males for 'social + male' trials, 11/11 males for 'predator' trials), and were performed primarily by resident males. Tail waves last an average of 2.11 (±0.09 SE) seconds. These behaviours will need to be further explored to determine their function.

#### DISCUSSION

Skinks are thought to lack social displays, and many species are less territorial and more fossorial than are other lizards (Stamps, 1977). However, *C. jarnoldae* used visual signals such as dorsolateral orientations, slow motion behaviour and throat flashes to communicate with conspecifics. We also observed males fighting, and chasing each other around the enclosures and out from under the shelters. Tongue flicks were also used, maybe to detect chemicals on, or left by, conspecifics (Alberts & Werner, 1993; Cooper, 1996; Cooper *et al.*, 1999). *Carlia jarnoldae* is a highly interactive, surfaceactive species that uses a wide array of visual and chemical signals to communicate with both conspecifics and predators.

Many of the behaviours performed by C. jarnoldae were similar to those described for other skinks (Carpenter & Ferguson, 1977; Torr & Shine, 1994; Whittier, 1994), but leg waves, which have been observed in other skinks (Carpenter & Ferguson, 1977; Whittier, 1994), were not observed in C. jarnoldae. We observed throat flash and letisimulation behaviours that have not been described in skinks before. Letisimulation was observed only in response to being captured, suggesting that it has an antipredator function. Throat flash behaviour displays the males' gular coloration, which may provide information about age, sex and reproductive status, or may act as a signal of aggression. C. jarnoldae appears less likely to engage in physical contact during aggressive interactions than are other skinks (e.g. Sphenomorphus kosciuskoi Done & Heatwole, 1977), but instead rely more on challenge or threat displays and chasing opponents rather than on physical combat to settle disputes.

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#### **SHORT NOTES**

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## **REPRODUCTIVE** CHARACTERISTICS OF THE INSULAR LACERTID *TEIRA DUGESII*

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The endemic lizard of the Madeiran Archipelago (Portugal), *Teira dugesii*, was recently separated from the lacertid genus *Podarcis* after the phylogenetic revisions of Böhme & Corti (1993) and Mayer & Bischoff (1996), but has close affinities with this genus (Richter, 1980). Therefore, a close phylogenetic relationship with the other two species included by Mayer & Bischoff (1996) in the genus *Teira*, *Teira perspicillata* (formerly included in the genus *Podarcis*) and *Teira andreanszkyi* (which belonged before to the genus *Lacerta*) must be taken into account. Nevertheless, more recent studies show that these species do not form a strongly monophyletic clade (Oliverio *et al.*, 2000), although *T. dugesii* and *T. perspicillata* seems to be sister species (Harris & Arnold, 1999).

As in other species of insular lacertid, little information is available on the reproductive characteristics of *Teira dugesii* (Richter, 1986; Malkmus, 1995; Bosch & Bout, 1998), although studies on other aspects of its biology have been published (e.g., diet: Sadek, 1981; Davenport & Dellinger, 1995). The species presents a high level of polymorphism both within and between islands, mostly in pigmentation (Cook, 1979; Crisp *et al.*, 1979), but also in body size, body proportions and scalation (Báez & Brown, 1997). Three subspecies have been described, the one that lives on the island of Madeira being the nominal form, and also the most robust and largest one (Bischoff *et al.*, 1989).

Teira dugesii is distributed throughout the archipelago, with very high densities over most of the island of Madeira (Dellinger, 1997). It occupies a great range of habitats, from sea level (including the intertidal zone: Davenport & Dellinger, 1995) to high areas in the mountains (up to 1861 m), and from uncultivated areas, with "laurisilva" (laurel woods), to the interior of the towns. It is more abundant in rocky areas, without dense or tall vegetation (Dellinger, 1997). Recently an introduced population has been detected in the city of Lisbon, Portugal (Sá-Sousa, 1995). *Teira dugesii* is omnivorous, feeding on invertebrates, leaves, nectar and fruits (Elvers, 1977, 1978; Sadek, 1981; Beyhl, 1990; Davenport & Dellinger, 1995).

The purpose of this note is to present and discuss data on some reproductive traits of this species, especially the relationships between female size and the number and size of eggs and hatchlings. This study was carried out with live animals that mated, laid eggs and produced hatchlings under controlled, captive conditions.

Lizards were captured by hand and with a noose in areas around the city of Funchal (island of Madeira :  $17^{\circ}$  0' W, 32° 45' N) in May 1995. These animals were transferred to terraria at La Coruña (Spain), where they were kept throughout the period of reproduction. The island of Madeira enjoys a very diverse climate, mainly conditioned by wind direction and altitude. La Coruña, located at sea level, has a distinctly Atlantic climate, very similar to the climate of the Madeiran coast (Carballeira *et al.*, 1983).

The study of captive animals was performed in three outdoor, open-air terraria measuring  $60 \times 40 \times 40$  cm, under natural conditions of light and temperature. These terraria were exposed to direct sunlight, so shade was provided over approximately one third of their surface, to allow the lizards to thermoregulate. The floors of the terraria were covered with 2 cm of gravel, over which stones and bark pieces were placed to provide shelter. Lizards were fed small pieces of fruit daily (banana, tomato, apple and figs) and live insects twice a week (*Tenebrio molitor* larvae, ant pupae and grasshoppers – nymphs and imagos of various acridid and tettigoniid species). Water was supplied *ad libitum*.

Twenty-six female lizards, which were individually marked by toe clipping, were introduced into the terraria on 5 May 1995, and observed daily thereafter. Sex, snout-vent length (SVL: to 0.1 mm, checked by double measurements), body mass and tail length were recorded for each animal. The reproductive state of each female was determined periodically by ventral palpation in order to detect the presence of eggs in the oviducts. When eggs were detected, females were removed and placed individually in  $10 \times 10 \times 20$  cm plastic boxes, filled to a depth of about 15 cm with soil, where eggs were laid. Immediately after laying, the female and each egg were weighed to 0.001 g precision. The number of eggs and their lengths and widths were also recorded. Egg volume was estimated as  $V=4/3\pi a^2b$ , where  $a=\frac{1}{2}$  width and  $b=\frac{1}{2}$  length. Egg characteristics were in all cases determined within 8 hr of laying. Each clutch could be unequivocally assigned to an individual female, allowing calculation of relative clutch mass (RCM) as the mass of the clutch (immediately after laying) divided by the mass of the spent female.

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#### SHORT NOTES

TABLE 1. Reproductive traits and adult female body size (snout-vent length, SVL) of *Teira dugesii* from Funchal, Madeira island. These traits were obtained from vivarium-laid eggs and from hatchlings hatched in a vivarium. Hatchling data correspond to the mean value for each clutch.

	Mean±SD	Min.	Max.	n
Female SVL (mm)	60.8±5.4	49.9	69.5	25
Female body mass (g)	4.84±1.63	2.72	8.40	21
Female condition	7.90±2.02	4.72	12.09	21
Clutch size	2.44±0.77	2	5	25
Clutch mass (g)	1.464±0.334	1.050	2.100	16
RCM	0.338±0.077	0.205	0.489	16
Egg mass (g)	0.658±0.103	0.525	0.925	16
Egg volume (mm <sup>3</sup> )	552±106	395	814	18
Hatchling SVL (mm)	30.9±1.3	29.1	33.4	11
Hatchling condition	2.06±0.35	1.53	2.65	11
Hatchling mass (g)	0.641±0.133	0.454	0.885	11



FIG. 1. The relationship between clutch size (number of eggs) and female snout-vent length (SVL) in *Teira dugesii*.

Each clutch was incubated in its plastic box near an open, south-facing window (see Galán, 1997). After hatching, the SVL, mass and sex of the hatchlings were recorded. Sex could be determined on the basis of dorso-lateral lines, which are evident at hatching in females but not in males. Sex was confirmed when animals reached sexual maturity.

Reproductive traits observed in the sample of *Teira dugesii* are summarized in Table 1. Clutch size (Fig. 1), mean egg size (volume and mass) and total clutch mass (Fig. 2) were all heavily dependent on female body size



FIG. 2. The relationship between total clutch mass and female snout-vent length (SVL) in *Teira dugesii*. The mass of each egg mass was measured immediately after oviposition.

(Table 2). However, there was not a significant relationship between female SVL and RCM. Larger eggs gave rise to larger hatchlings (Fig. 3), but neither the SVL nor the body mass of hatchlings was significantly correlated with female size (Table 2). There was no significant difference between the mean sizes of male and female hatchlings (Table 3).

The mean RCM observed in *Teira dugesii* is similar to that of several continental populations of *Podarcis* species, which have a larger clutch size (Braña *et al.*, 1991). This is in accord with the idea of a relative stabil-

TABLE 2. Summary of linear regression analyses of reproductive traits on female snout-vent length (mm) in Teira dugesii.

Reproductive trait	<i>R</i> <sup>2</sup>	F	df	Р	intercept	slope
Clutch size	0.29	9.30	1,23	0.006	-2.18	0.08
Clutch mass (g)	0.49	13.54	1,14	0.002	-1.18	0.04
Mean egg volume (mm <sup>3</sup> )	0.24	4.94	1,16	0.041	-3.35	9.16
Mean egg mass (g)	0.37	8.18	1,14	0.013	-0.05	0.01
Relative clutch mass	0.18	3.17	1,14	0.097	0.71	-0.01
Mean hatchling SVL (mm)	0.02	0.21	1,9	0.660		
Mean hatchling mass (g)	0.01	0.09	1,9	0.773		



FIG. 3. The relationship between the mean snout-vent length (SVL) of hatchlings and mean egg volume in 10 clutches of *Teira dugesii* (r=0.62, P<0.05).

ity of RCM among lizards (Vitt & Congdon, 1978; Vitt & Price, 1982).

Rykena & Bischoff (1992) found a positive correlation between female body mass and clutch mass in *Teira* andreanszkyi, and a positive correlation between RCM and clutch size. We found no significant relationship between RCM and clutch size in *Teira dugesii* ( $R^2$ =0.07; F=1.09; df=1,14; P=0.314).

We observed double-clutching in three large *T.* dugesii (SVL: 63.8, 66.2 and 66.9 mm respectively), which laid for the first time in May and for the second time in July (two) or August (one). The average period between two consecutive layings was 64.3 days (range: 53-71 days). Matings were observed in these females 20 to 28 days (mean = 24.7 days) after the first laying and 41 to 50 days (mean = 46.0 days) before the second laying. The characteristics of each female's first and second clutch were similar: the clutch size was the same (3 eggs in one case and 2 in the other two) and the characteristics of the eggs and of their hatchlings did not differ significantly. In captive, fully-grown females of *Teira andreanszkyi*, Rykena & Bischoff (1992) detected up to six clutches in one breeding season.

The few published data on the reproduction of *Teira* dugesii are from Richter (1986), according to whom the laying period is May-August, with a clutch size of two or, exceptionally, three eggs. The laying period we observed was similar. It lasted for four months in 1995, from May to August. Clutch size varied significantly among these months ( $F_{3,25}$ =3.73, P=0.026; Table 4), though the size (SVL) of reproductive females did not ( $F_{3,25}$ =1.97, P=0.15). This laying period is longer than for the majority of temperate lacertid species, in which

TABLE 3. Summary statistics of snout-vent length (SVL) and body mass of male and female hatchlings of *Teira dugesii*. Measurements were in all taken within 24 hr of hatching.

	Mean±SD	Min.	Max.	n
Hatchling SVL (mm)				
male female	30.9±1.8 30.9±1.0	28.7 29.1	33.6 33.4	12 21
Hatchling body mass (g)				
male female	0.645±0.158 0.598±0.099	0.436 0.471	0.891 0.871	12 21

laying usually lasts for three months, ending in July (Bauwens & Díaz-Uriarte, 1997). However, another insular lacertid, *Podarcis pityusensis*, was reported to have a laying period coincident with that which we observed in *Teira dugesii*, i.e. May-August (Carretero *et al.*, 1995).

In *T. dugesii*, the clutches consisted of few, largesized eggs. At the moment of laying, the eggs were elongate, the width of the largest reaching only 40% of the length (mean = 51.7 %, range: 40%-60%, n=32). In *Teira perspicillata* (Doumergue, 1901; Richter, 1986; Schleich *et al.*, 1996), as in *Teira andreanszkyi* (Rykena & Bischoff, 1992), eggs are also cylindrical and elongate. Such a large egg size in a relatively small-sized lizard may constrain the eggs to have a cylindrical shape, differing considerably from the usual oval shape in the lacertids (e.g. Arnold & Burton, 1978; Bruno, 1986). This cylindrical shape arises from the morphological constraint imposed by the female's pelvic girdle (Sinervo & Licht, 1991).

The most frequent clutch size in *Teira dugesii* was two (17 cases in 25), and this number was observed in smaller adult females as well as in the larger ones, although some of the latter had clutches of up to five eggs (Fig. 1).

Very small clutch sizes and large eggs have been observed in insular species or populations of the closely related genus *Podarcis* (Vicente, 1989; Carretero *et al.*, 1995; Castilla & Bauwens, 2000*a*,*b*). Thus, in *Podarcis pityusensis* from the Mediterranean island of Ibiza, average clutch size is 2.3 eggs (range: 1-4) and average egg volume is 394 mm<sup>3</sup> (Carretero *et al.*, 1995). *Podarcis carbonelli berlengensis* from Berlenga Island

TABLE 4. Female snout-vent length (SVL, in mm) and clutch size of *Teira dugesii* in each of the four months of the laying period (SEM = standard error of the mean).

Month	Female SVL (mean±SEM)	Range	Clutch size (mean±SEM)	Range	n
May	63.0±1.9	55.0-69.5	2.37±0.18	2-3	8
June	63.7±1.5	58.7-68.2	3.14±0.40	2-4	7
July	59.6±2.2	54.7-66.9	2.14±0.14	2-5	7
August	57.0±2.8	49.9-63.8	$2.00 \pm 0.00$	2	6

(Portugal) has an average clutch size of 2.01 eggs (range: 1-4), and average egg and clutch masses of 0.43 g and 0.88 g, respectively (Vicente, 1989). *Podarcis atrata* from the Columbretes Islands (Spain) has an average clutch size of 2.8 eggs (range: 1-5), and average egg and clutch masses of 0.37 g and 1.04 g (Castilla & Bauwens, 2000*a*). The average size of the reproductive females in these lacertids is similar to that observed in *Teira dugesii*.

Teira perspicillata and Teira andreanszkyi also have very small clutch sizes, in spite of the fact that these are not insular species. Thus, *Teira perspicillata* lays two to three eggs (Doumergue, 1901; Richter, 1986; Schleich *et al.*, 1996) and *Teira andreanszkyi* lays one to three: Busack (1987) has detected two to three (mean = 2.1) while Rykena & Bischoff (1992) observed one to two (mean = 1.6) varying between 0.264 g and 0.340 g.

Our sample of *Teira dugesii* had similar clutch sizes to some insular *Podarcis* populations, but the average size of *T. dugesii* eggs was much larger. The large size of the eggs was also related to the large size of the hatchlings (Fig. 3), suggesting a tendency towards maximization of size at hatching (see also Sinervo, 1990; Frankenberg & Werner, 1992). In this process, the lizard of Madeira seems to have advanced much further than insular populations of *Podarcis*, excepting *P. lilfordi* (Table 5). The high level of morphological polymorphism described in *Teira dugesii*, as well as the wide range of habitats that it occupies in the Madeiran Archipelago (Cook, 1979; Báez & Brown, 1997; Dellinger, 1997) may lead to some variability in reproductive traits. The present paper deals only with populations in the Funchal area, although it is probable that the general reproductive traits observed – such as long laying period, small clutch size and large eggs and hatchlings – occur in other populations of this archipelago.

The data of the present paper point towards two alternative explanations for the reproductive characteristics of T. dugesii. If the genus Podarcis is used as a basis for comparison, then the data provided by this work suggest that the reproductive traits of the studied population are an adaptation to insularity. On the other hand, if we accept as true the close phylogenetic relationship between the lizards of the island of Madeira and the genus Teira (sensu Mayer & Bischoff, 1996), and we compare its reproductive characteristics with the two species of Teira from North Africa, then the present results suggest that phylogenetic relationships rather than mere adaptations to insular conditions may account for the relatively small clutch size. However, as far as egg size is concerned, Teira dugesii could be viewed as an insular Teira.

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TABLE 5. Reproductive traits of some continental and insular lacertid lizards (*Podarcis* spp. and *Teira* spp.). SVL: mean or range of female snout-vent length (mm); Clutch size: number of eggs [range (mean)]; Egg vol.: mean egg volume (mm<sup>3</sup>); Egg mass: mean egg mass (g).

Species	Location	SVL	Clutch size	Egg vol.	Egg mass	Reference
(A) CONTINENTAL						
P. muralis	Asturias	59.8	4-7(5.6)	-	0.27	Braña <i>et al</i> . (1991)
P. muralis	<b>Basque</b> Country	60.0	3-7(4.9)	-	0.28	Braña <i>et al.</i> (1991)
P. bocagei	Galicia	53.3	2-7(4.1)	236	0.26	Galán (1997)
P. bocagei	Asturias	55.4	3-4(3.3)	-	0.26	Braña <i>et al</i> . (1991)
P. hispanica	Asturias	51.8	1-3(2.3)	-	0.30	Braña <i>et al</i> . (1991)
P. hispanica	Salamanca	61.3	(3.6)	-	0.34	Castilla & Bauwens (2000a)
T. perspicillata	Morocco	50.6	-	283	-	Schleich et al. (1996)
T. perspicillata	Morocco	59.8	2-3	-	-	Richter (1986)
T. perspicillata	-	- ,	-	351	0.38	Bosch & Bout (1998)
T. andreanszkyi	Morocco	40-48	1-2(1.6)	256	0.30	Rykena & Bischoff (1992)
T. andreanszkyi	Morocco	44-53	2-3(2.1)	-	-	Busack (1987)
T. andreanszkyi	-	-	-	276	0.31	Bosch & Bout (1998)
(B) INSULAR						
P. carbonelli berlengensis	Berlenga	57.0	1-4(2.0)	389	0.43	Vicente (1989)
P. atrata	Columbretes	63.1	1-5(2.8)	346	0.37	Castilla & Bauwens (2000a)
P. pityusensis	Ibiza	57.5	1-4(2.3)	394	-	Carretero et al. (1995)
P. lilfordi	Cabrera	61.9	2-4(2.5)	550	0.63	Castilla & Bauwens (2000b)
T. dugesii	Madeira	60.8	2-5(2.4)	552	0.66	This work

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## HABITAT USE, EGG LAYING SITES AND ACTIVITY PATTERNS OF AN ENDANGERED MAURITIAN GECKO (PHELSUMA GUENTHERI)

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Günther's gecko, *Phelsuma guentheri*, is an endangered gecko that was endemic to the Mascarene Islands but is now confined to Round Island, a small island 20 km off the northern coast of Mauritius (Merton *et al.*, 1989). Estimates of population size vary greatly from 1500-1800 (Vinson, 1975), to only 180-550 individuals in 1982 (Bullock, 1986) and has remained small (D. J. Bullock, pers. com.) despite goats (*Capra hircus*) and rabbits (*Oryctolagus cuniculus*) being removed in 1978 and 1986 respectively, resulting in increasing vegetation cover (North *et al.*, 1994).

The survival of Günther's gecko has depended largely on the absence of introduced predators, such as rats (Rattus norvegicus, R. rattus) (Cheke, 1987) and accidental introduction of such species is an ongoing risk. Due to this risk - or that of a catastrophic stochastic event and the small population size - translocation of geckos to neighbouring islands was suggested (Merton et al., 1989; Dulloo et al., 1997). Phelsuma guentheri has been considered a primitive day-gecko (Vinson & Vinson, 1969; Staub, 1993), and it differs from other members of its genus by its larger size, duller coloration, and a number of other, less conspicuous morphological features (Vinson & Vinson, 1969). However, insufficient knowledge exists on the behaviour and ecology of the species. For example, the activity pattern of Günther's gecko has been described as diurnal (Vinson & Vinson, 1969; Vinson, 1975), crepuscular (Bloxam & Vokins, 1978; Staub, 1993), and nocturnal (Bullock, 1986). There are also conflicting descriptions of its feeding habit (insectivorous, herbivorous, nectivorous, or carnivorous), habitat use (terrestrial or arboreal), and choice of egg laying site (Vinson & Vinson, 1969; Vinson, 1975; Bullock, 1977, 1986; Bloxam & Vokins, 1978; Bullock & North, 1991).

The aim of the present study was to provide quantitative information on the behaviour and ecology of P. guentheri, to clarify some of the uncertainties concerning this species. We focused on two specific aspects, namely habitat use and egg laying site characteristics, which were investigated through surveys of all habitats on Round Island. The information gathered here should allow a more objective evaluation of the behaviour and ecology of *P. guentheri*.

Round Island (longitude 57°47'03"E, latitude 19°54'03"S) measures only 187 ha in area (Carpenter, 1998) and lies 281 m above sea level at its highest point (Merton et al., 1989). Its relative isolation and difficult access helped to protect its native fauna, creating a refuge for eight reptiles, including six lizards (Leiolopisma telfairi, Gongylomorphus bojerii, Cryptoblepharus boutonii, Phelsuma ornata ornata, Phelsuma guentheri, Nactus serpensinsula durrelli) and two snakes (Casarea dussumieri and Bolyeria multocarinata; Bullock, 1986). Access to the island is by permit only and is limited to seven consecutive days. Two one-week visits were made during this study: a preliminary visit in April 1998, and a survey visit in May 1998. An aerial photograph of Round Island in 1991 was obtained from the Department of Housing and Land Use (Port Louis, Mauritius) and enlarged to a scale of 1:200,000. All parts of the island were classified into one of five main habitat types: (1) rock, (2) creeper, (3) grassland, (4) palm rich forest, (5) Lomatophyllum spp. The area of each habitat was measured by overlaying the map with a fine-scale grid (equivalent to 25 m x 25 m quadrats) and allocating each quadrat to a habitat. Due to time constraints, one hundred and five quadrats (out of a possible 2995) were chosen at random prior to visiting Round Island with sampling stratified so that the number of quadrats in each habitat was proportional to the area covered by that habitat. During the rainy season, from 14 May to 21 May 1998, each randomly chosen quadrat was surveyed by one of five recorders for both vegetation and presence of P. guentheri or other saurian species. The position of each quadrat was marked, and percentage cover of the stratified vegetation layers were assessed visually using a six-category Braun-Blanquet scale (Bullock, 1997), to which a category of 0% cover was added. Each quadrat was searched for a period of 30 min. For each P. guentheri sighted, the following variables were recorded: time of sighting, activity (resting, i.e. motionless with head down, vigilant, i.e. motionless with head up, stalking, walking, feeding/drinking), substratum on which the individual was first observed (e.g. rock, Latania, Pandanus) as well as microsite choice (e.g. rock face or overhang, Latania frond, crown or trunk, etc.) and aspect (recorded with a compass), vertical distance above ground (estimated visually), and presence of, and distance to, any other lizard species. Searches for P. guentheri were carried out twice in each quadrat: once during daylight (06.00-18.00 hr) and once at night (18.00-06.00 hr).

In each quadrat, the daylight search for geckos was followed by a search for egg-laying sites. Female P. guentheri attach their eggs to various surfaces, and prominent egg scars remain on the substratum after the

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eggs have hatched (Bloxam & Vokins, 1978; Osadnik, 1984; Jones, 1988). Some egg-laying sites appear to be communal and traditional, as judged by the great number of egg scars in discrete clusters and the overlap observed among egg scars, which suggests repeated use from year to year (Vinson & Vinson, 1969; Jones, 1988). Whenever such egg scars were found, we recorded substratum type, vertical distance to the ground, evidence of previous site use (by counting the number of egg scar overlaps), number of discrete egg clusters and surface area of each cluster, and microsite choice and aspect (as above). The total area of each egg laying site was obtained by summing the areas of all clusters present at that site.

The predominant habitat of Round Island, based on the 1991 aerial photograph, was bare rock, which covered just over half (52.4%) of the island. However, an examination of the vegetation scores obtained for the 105 randomly selected quadrats reveals an increase in vegetation cover since 1991. Indeed, while bare rock should have scored only very low values on the Braun-Blanquet scale, this habitat scored mainly non-zero values in herb (98% non-zero scores) and canopy layers (88.7% non-zero). Two of the three ground-cover habitats, - creeper and grassland - showed, as expected, mostly very low values of canopy cover (creeper: 100% of scores < 1; grassland: 93.3%). However, the third ground-cover habitat, Lomatophyllum, scored only nonzero values for the canopy layer. This suggests that the habitat designation used, although useful in establishing the initial sampling design, was not an accurate descriptor of the current state of habitats encountered in quadrats classified as rock and Lomatophyllum.

In over 100 hours spent surveying, Günther's geckos were sighted 25 times. There were significantly more sightings during the day (n=18, 72%) of the total sightings) than at night (n=7, 28%); G=4.61, df=1, P<0.05). However, sighting rates (number of sightings per survey) did not differ between day and night (Mann-Whitney U test; U=4.00, n=7, P=0.63). Adult P. guentheri were recorded in 17% (18/105) of all quadrats surveyed. All quadrats with P. guentheri were originally classified either as rock (48% of sightings) or palm rich forest (52%). There were significantly more sightings in palm rich forest than expected based on the availability of this habitat (G=10.67, P<0.05).

When initially sighted, *P. guentheri* was observed significantly more often on *Latania* palm (n=18, 72% of sightings), and less frequently on rock (n=5, 20%) or *Pandanus* (n=2, 8%;  $\chi^2=17.43$ , df=2, *P*<0.001). On *Latania*, *P. guentheri* was found either on the trunk (20% of sightings during the day, 33.3% at night), crown (day: 46.7%, night: 33.3%), or fronds (day: 33.3%, night: 33.3%). There was a significant difference between daytime and night-time microsite choice on *Latania* (n=18, U=9, P=0.05). By contrast, the two *P. guentheri* seen during the day on rock were under an overhang, while the three individuals sighted on rock at night were on the exposed rock face. The overall mean vertical height above ground of arboreal sightings was 2.5±1.5 m (mean±SD, n=19), with the mean height on Latania (2.7±1.5 m, n=17) being greater than the mean height for Pandanus (1.3±0.5 m, n=2).

The majority (14/25, 56%) of *P. guentheri* appeared to be resting at the time of sighting. Active geckos were either vigilant (6/25, 24%), walking (4/25, 16%), or stalking *P. ornata* (1/25, 4%). There was one record of predation on *P. ornata* by *P. guentheri*. There was no significant difference in gecko activity among macrosites ( $\chi^2$ =4.39, df=2, *P*=0.09), and there was no difference in proportion of active geckos between day and night-time ( $\chi^2$ =0.68, df=1, *P*=0.45).

One or more of three other saurian species were recorded with 16 (64%) of the *P. guentheri* sightings. These included ornate day gecko, *P .ornata* (eight sightings; all diurnal), Durrell's night gecko, *Nactus serpensinsula durrelli* (five sightings; four diurnal, one nocturnal), and Telfair's skink, *Leiolopisma telfairi* (three sightings; two diurnal, one nocturnal).

A total of 31 *P. guentheri* egg-laying sites were found. Rock was the substrate most commonly used (15/31 sites, 48.4%), followed by *Pandanus* branches (10 sites, 32.3%) and *Latania* fronds (six sites, 19.4%). Egg-laying sites were always off the ground (overall mean±SD vertical height:  $1.67\pm0.72$  m), although there was no significant difference in egg laying site height among the three habitats (Kruskal-Wallis test, *H*=2.00, *n*=3, *P*=0.37). In the majority of cases (83.8%), the egg laying sites were concealed either under rocky overhangs or on the underside of *Latania* fronds and *Pandanus* branches.

The number of egg scar overlaps increased with egg cluster area ( $r_s=0.75$ , n=18, P=0.0004), suggesting that larger sites have had a longer history of use. Egg laying sites on rock were significantly larger (Kruskal-Wallis test, H=17.5, n=3, P<0.001) and had significantly more egg scar overlaps than egg laying sites on either *Latania* or *Pandanus* (Kruskal-Wallis test, H=9.9, n=3, P=0.007). The orientation of egg laying sites was not random ( $\chi^2=8.1$ , df=3, P=0.04). Most sites faced a northerly direction (sample mean direction  $\pm$  95% CI: 346.4 $\pm$ 46°).

A total of 11 males and 3 females were captured, generating a sex ratio of 1 male : 0.27 female. Males and females did not differ in length (mean SVL±1 SD, males: 110.7±10.7 cm; females: 108.1±2.9 cm: n=14, z=0.39, P=0.70), weight (males: 59.3±17.0 g; females: 44.8±6.3 g; n=14, z=1.32, P=0.19), nor in scansor size (males: 5.0±0.8 cm; females: 4.7±0.3 cm: n=12, z=0.65, P=0.60).

Our results suggest that Günther's gecko is mainly arboreal in habit. It appeared to rely greatly on the native fan palm *Latania* for cover during both day and night, but egg-laying sites were located primarily on rock. We confirmed anecodotal evidence of saurian predation behaviour by *P. guentheri* (Vinson & Vinson, 1969; Bullock & North, 1991). The confusion surrounding the activity pattern of Günther's gecko, whether diurnal (Vinson & Vinson, 1969; Vinson, 1975), crepuscular (Bloxam & Vokins, 1978; Staub, 1993) or nocturnal (Bullock 1986, 1977), may stem from the fact that this species showed no distinct pattern of activity. We found no difference between day and night in the proportion of active geckos or in the type of activity undertaken during day or night sightings. Although more Günther's geckos were observed during the day in absolute terms, difficulty of finding geckos in the dark appeared to have been partly compensated by the more exposed location they adopted at night (e.g. *Latania* trunk instead of crown, rock surface instead of overhang).

The arboreal habit of Günther's gecko was clear during this field study. As was suggested by Bullock (1986) and North *et al.* (1994), this species appears to prefer palmrich forest to other habitats. On a smaller scale, *P. guentheri* was recorded significantly more often on *Latania* than on rock or *Pandanus*. However, since the relative availability of these substrata is not known, it is difficult to say whether this pattern actually represents habitat choice. Nevertheless, the scansor size of *P. guentheri*, relative to its body size, is consistent with that of other arboreal congeners (Russell, 1975, 1985; Carpenter, 1998), supporting the suggestion that Günther's gecko is primarily arboreal.

At first glance, the reliance of Günther's gecko on Latania does not appear to be related to reproduction. Nearly half of all egg-laying sites were found on rock (see also Vinson & Vinson, 1969; Vinson, 1975; Bloxam & Vokins, 1978), and less than one-fifth were on green fronds of Latania. However, while rock is a permanent feature of the environment, Latania fronds are temporary in comparison. It is not surprising that egg laying sites on rocks were larger and had a longer history of use (i.e. more egg-scar overlaps) than those on other substrata. This may not indicate a true preference for rock as egg laying site but may be a reflection of the historical unavailability of other sites. Indeed, as recorded in this study and by North et al. (1994), the vegetation of Round Island has been recovering since the extirpation of rabbits and goats. Prior to grazer removal, egg-laying sites on vegetation were probably extremely limited, possibly explaining the repeated use of rock surfaces for reproduction. It will be interesting in the future to monitor the relative use of rocky and vegetation sites by breeding Günther's geckos as vegetation recovery continues.

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#### **BOOK REVIEWS**

Horned Lizards, revised edition. Jane Manaster. (2002). 84 pp. Texas Tech University Press, Lubbock. £17.95 (paper).

Introduction to Horned Lizards of North America,  $2^{nd}$  edition. Wade Sherbrooke. (2003). 178 pp. California Natural History Guide No. 64. University of California Press, Berkeley, Los Angeles and London. £10.95 (paper).

Horny toads are not your typical lizards. Squat, round, with tiny spikes on their backs and around the nape of the neck, horned lizards (*Phyrnosoma* spp.) actually do look like toads lurching off into the underbrush. With spikes above their eyes making them look as if they are scowling, and a wide jawline giving them a frown, they are undeniably charismatic. If you have ever seen one of these scuttling along, you will understand why they are so beloved across time and cultures.

Horned Lizards by Jane Manaster is a sweet little book about these odd lizards. Written by a historian, it is evident she is passionate about these creatures. She has trawled through historical documents from early explorations to more recent by-gone days in Texas, providing anecdotes and quotes from native American, Mexican, and Texan folklore. She includes a section on the biology and geographical distribution of the horned lizards, although the book is not intended as a field guide. There is an extensive chapter on conservation threats to these species, discussing impacts from collection, loss of habitat, and introduced ant species. Charmingly written, this at times whimsical book is an introduction to the lives and folklore of these lizards, aimed at a largely non-scientific audience. I would probably give this book to my mother in an attempt to help her find an understanding and appreciation of these lizards.

For myself, however, I would buy Wade Sherbrook's book *Introduction to Horned Lizards of North America*. This is a wonderful book. I remember sitting in a cantina in Mexico with the author in my first summer in the US, listening to him describing horned lizard burrowing behaviour. He was so passionate and thrilled about what he was describing, and this excitement comes through in his writing.

I had a little trouble getting started on reading this book from the beginning, because there are beautiful and astonishing illustrations on nearly every page. I thumbed though it time and again, reading sections that caught my eye before returning once again to the beginning. The photographs are certainly memorable, most of them taken by the author himself.

In the Natural History section Wade covers all aspects of herpetology, including geophylogeny, reproduction, thermoregulation, foraging and diet, parasites (lavishly illustrated with some lovely gross-out photos of stomach contents, worms and other inner bits!), and predation and defence. Much of the information contained here is applicable to lizards and indeed reptiles in general, and he provides examples of horned lizard adaptations. The descriptions of horned lizard defence behaviour, and the accompanying photographs, are worth possession of this book alone!

There is also a section entitled Humans and Lizards, with the folklore and cultural references included. Wade discusses some of the conservation threats to horned lizards, but only briefly. The threats are the same as those outlined by Jane Manaster: collection, habitat loss, introduced ants.

The book is constructed like a field guide, with silhouettes of the horn arrangement of each species on the inside covers as an identification guide, and a thorough section on each of the *Phrynosoma* species in both the United States and Mexico, with range maps and identification descriptions. The book is sturdy enough to withstand field use.

This book should be a fantastic inspiration to young budding biologists, and not just those interested in herpetology. Wade writes with a clarity and depth that anyone can follow. Perfect for the lay-person who only occasionally encounters these lizards and wants to know a little more, this book would also be excellent recommended reading for undergraduates and postgraduates alike, and it is a must-have for the herpetologist. It kept me enthralled from cover to cover, and I certainly learned a great deal from it. Do your kid a favour, buy her this book! Just make sure you read it before handing it over.

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Sea Dragons: Predators of the Prehistoric Oceans. Richard Ellis (2003). 313+vii pp. University of Kansas Press. US\$29.95 (cloth).

Many years ago I was shown a photograph of a small ichthyosaur fossil by the late Beverly Halstead who asked me whether I thought this embryo was enclosed in any membranes. My response was to suggest that it would be better to ascertain whether the specimen was really an embryo. Subsequent investigations by myself, Dave Unwin and Manabe Makoto did reveal that this individual (and most other small ichthyosaurs within the body cavity of larger specimens), was an embryo and our publication finally confirmed that this group of ancient marine reptiles were viviparous. There started my long-standing interest in ichthyosaurs and other marine reptiles of the Mesozoic, but finding an accessible account of the fossil record and presumed biology of these groups has proved difficult.

Whilst searching the Internet for details of the book to accompany a BBC series (Sea Monsters – A Walking with Dinosaurs Trilogy, November 2003) I was pleased to find that Richard Ellis had produced a "popular" account of ancient marine reptiles. Perhaps, at last there would be a book that dealt with the diversity of these species and brought them to life in the same way that other countless books have done for dinosaurs?

This book is split into seven chapters. The first two introduce the popular and scientific idea of "sea dragons" and give some indication of their origins. The next four chapters are each dedicated to one of the four major groups: ichthyosaurs, plesiosaurs, pliosaurs and mosasaurs. The final chapter briefly considers the reasons why these groups of reptiles did not survive beyond the Cretaceous-Tertiary boundary, 65 million years ago. The text forms 260 pages of the book with a further 30 pages of references. The index is quite effective.

Drawing on a wide variety of sources (including personal communications with palaeontologists working on the animal groups) Ellis has tried to cover all topics with descriptions and history of the fossil record of each type of reptile together with the debate surrounding the lifestyle of each group. Indeed debate is a feature of the text - contrasting views about a variety of topics are presented - but at times the debate is simply reproduced verbatim from the original sources. In fact, a lot of the book was lifted directly from publications by other authors and whilst the authors are given full credit, I found the constant quotation of other people's work got rather tedious. Unfortunately, I found that the chapters dealing with each group tended to meander along without any obvious thematic thread - there was no obvious evolutionary, temporal or functional separation of the biology of any of these reptile groups. I felt that the lack of subheadings in chapters made reading the book feel like a bit of a slog. There is also liberal use of footnotes, often used to good effect to describe technical points or add more information.

The book is illustrated with scattered line drawings of the different types of reptiles, the standard of which I found rather disappointing. Ellis is credited as being an artist of some standing and yet he has largely failed to breathe any life into the subject of his illustrations. It is the lack of informative illustrations that makes this book less accessible to the enthusiastic amateur. I found it very curious that the entire book does not contain one photograph of a real fossilised animal. This is despite marine reptiles being some of the best examples of extinct animals preserved fully articulated, and the constant reference to fossil specimens. Moreover, there are almost no drawings to illustrate the technical points described and so the reader is left to imagine many of the contrasting issues. For instance, locomotion in plesiosaurs and pliosaurs has been the subject of a lot of debate for many years – were the flippers moved up and down like wings or backwards and forwards like oars? The reader would have found that some line drawings of the actions involved - and the forces that they supposedly generated - would have made the distinction between these two actions much easier. It would have also been great to have sketches of the body plan and skeleton of each type of animal.

I was left wondering about so much of the diversity of these reptiles. For example, m how many species/genera are recognised and how are related? Where did the different species live and when? The information is there in the text but there is no overview of any particular group that would help summarise their context in the world and the fossil record. Tables of this information would have also helped to break up the text.

This book may have been aimed at reviewing the existing information for the palaeontologists working in this field but I am sure that Ellis wrote this book with the intention of bringing these fascinating species to the attention of a wider audience, particularly those already keen on those other Mesozoic reptiles, the dinosaurs. It is difficult to fault the content of the book, it is certainly up to date, but the way that the information is presented suggests that the target audience was not well thought out. Amateurs interested in the fossil record do not always have the zoological or geological background that would make this book more readable. Provision of more supporting formation (e.g. a list of the sequence of geological eras) and drawings and photographs that illustrate important points would have made this book more accessible. From a more academic perspective this book provides a useful single reference of much of the literature about ancient marine reptiles, and hence I find it of value and interest, but whether it provides any further novel insights into these animals is uncertain.

My criticisms about this book are mainly about the presentation of the content rather than the text *per se*. I guess that my disappointment lies in what I see as a missed opportunity to portray these exceptionally interesting animals to a wider audience. Nevertheless I am inclined to recommend this book. Despite the faults in presentation it is full of useful and interesting information and it is an attempt to describe the life and death of ancient marine reptiles in a realistic way.

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## THE HERPETOLOGICAL JOURNAL

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- 5. The usual rules of zoological nomenclature apply.
- 6. Tables are numbered in arabic numerals, e.g. TABLE I; they should be typed double spaced on separate sheets with a title/

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  - Bellairs, A. d'A. (1957). Reptiles. London: Hutchinson.
    Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared 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 Journal of Physiology* **216**, 995-1002.
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- 12. All submissions are liable to assessment by the editorial board for ethical considerations, and publication may be refused on the recommendation of this committee. Contributors may therefore need to justify killing or the use of other animal procedures, if these have been involved in the execution of the work. Likewise, work that has involved the collection of endangered species or disturbance to their habitat(s) will require full justification.

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