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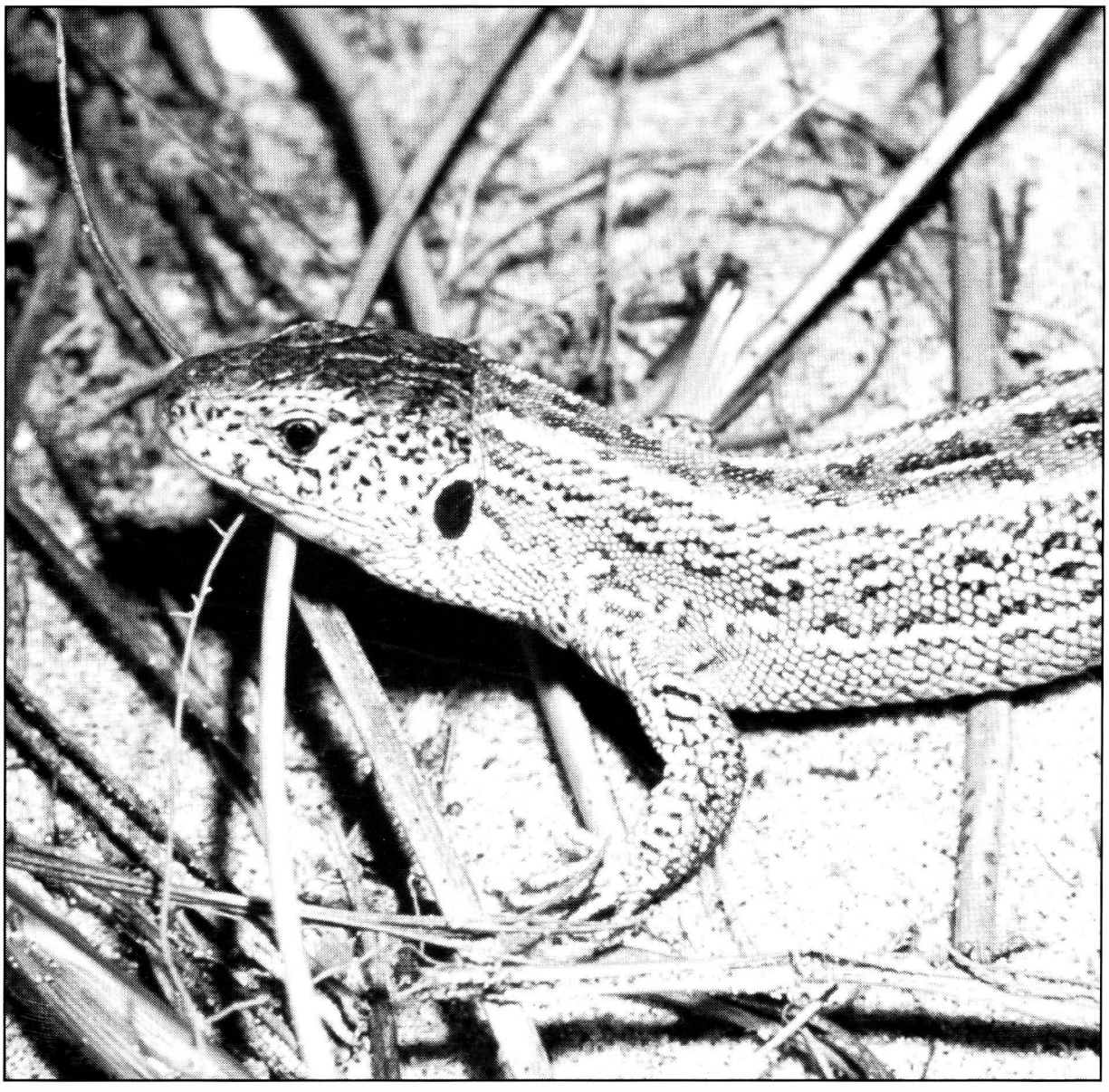

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FRONT COVER: Sand lizard, *Lacerta agilis* (S. Harrop).

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DEVELOPMENTAL ARREST IN *LEPTODACTYLUS FUSCUS* TADPOLES (ANURA: LEPTODACTYLIDAE) III: EFFECT OF LENGTH OF ARREST PERIOD ON GROWTH POTENTIAL

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Eggs of the neotropical frog *Leptodactylus fuscus* (Anura: Leptodactylidae) are laid in foamy masses in burrows close to sites of temporary pools. After hatching, the tadpoles make a new form of foam and, if no rain falls, enter a kind of developmental arrest. This may last around 30 days after egg deposition. In the experiments reported here, the ability of tadpoles to grow was tested after different periods of developmental arrest in foam nests. In the short term, tadpoles in foam for 15 days grew faster than those in foam 5 or 25 days (these grew at about the same rate). However, when raised to metamorphosis, a different pattern emerged. The longer tadpoles remained in foam, the slower they grew and the smaller the proportion that eventually metamorphosed. There was considerable variation between nests, with some showing high metamorphic potential 30 days after deposition but others low after only 18 days. Unexpectedly, size at metamorphosis varied with time spent in the nest. The longer tadpoles remained in the nest, the larger their mean size at metamorphosis, but also the greater their variability in size at metamorphosis. Some of the large tadpoles differed in shape from normal. Tadpoles allowed to grow soon after nest deposition grew rapidly to metamorphose at relatively smaller size and low variability. The significance of these results for the success of the developmental arrest strategy is discussed.

INTRODUCTION

Frogs of the *Leptodactylus 'fuscus'* species group (Heyer, 1978) deposit eggs in foam nests in burrows on land, near sites of temporary pools, generally in advance of heavy rains. In Trinidad, where we have studied *L. fuscus*, the wet season lasts about eight months, but is punctuated by dry spells of varying length when temporary pools may dry out. In species investigated so far, eggs develop past hatching but, in the absence of heavy rain, the tadpoles enter a form of developmental arrest (see Downie, 1994*a,b* for a detailed account of this phenomenon in *Leptodactylus fuscus* and for a review of our knowledge of other '*fuscus*' group species). If heavy rains fall during this period, the tadpoles are washed from their burrows and begin feeding. This mode of reproduction appears to have some advantages: when heavy rains fall, *L. fuscus* tadpoles enter the pool and are able to feed immediately, whereas most other amphibian species using the same pools are just beginning to deposit eggs. This allows *L. fuscus* tadpoles to feed on the eggs of other amphibians (Downie, 1988, 1990), and it also shortens the time that free-standing water must be available to allow metamorphosis to be reached, an important feature in areas with patchy and unpredictable rainfall.

This reproductive strategy may have some disadvantages. During the arrest period, the tadpoles remain active: they make a new kind of foam that replaces foam deposited by adults and actively wriggle within the foam (Downie, 1984, 1989). This activity requires resources: when the tadpoles enter developmental arrest, their gut endoderm is full of yolk granules; but after a few days, yolk content is greatly reduced, and is generally undetectable after two weeks. Furthermore, after three weeks of arrest, tadpoles begin to lose weight and eventually die, 27.5 days after egg deposition on average (Downie 1994*a*). It is clear that the ability to survive in the foam nest is limited and that if the adults breed too far in advance of significant rainfall, the entire clutch can be lost. Even before tadpoles die, they may have declined in body condition to a point from which they cannot recover. The experiments described in this paper were designed to test this prediction. Tadpoles were kept in foam for different periods of time, then their growth potential was assessed in two ways: (1) by determining survival to metamorphosis, size at metamorphosis, and development time; and (2) by measuring growth rate when given access to water and food.

MATERIALS AND METHODS

COLLECTION AND MAINTENANCE OF FOAM NESTS

Foam nests of *L. fuscus* were collected in July and August 1991 and 1993 from several sites in Trinidad, West Indies, mainly from a drainage ditch beside the main road to Piarco Airport in 1991, and from a ditch beside the recreation ground at Lopinot Village in 1993. At both sites the grass growing in and around the ditches was kept short, allowing easy access. The ditches filled quickly with water after heavy rain, but soon dried out if not replenished. Searches for foam nests were performed by inserting a spoon handle into

the mud of the side of the ditch, near the base, when the ditch was dry. Nest holes are generally not visible because they are plugged by the parents after deposition, but at Lopinot, a few incompletely plugged nests were found.

Only recently constructed nests with tadpoles at pre-foam-making stages were used, i.e. prior to Gosner (1960) stage 25. This is because it was important to know the time of egg deposition. Once tadpoles have entered developmental arrest, they do not progress beyond stage 28-29, and it is therefore impossible to tell the time of egg deposition from normal staging criteria (though it can be assessed approximately by histology: see Downie, 1994*a*)

After collection, nests were maintained in the laboratory on moist tissue paper in 250 ml polythene tubs, with the lids loosely attached to allow respiration but prevent evaporation. The tissue paper was replaced every few days. In Trinidad, the laboratory air temperature ranged from 27- 29°C. We have not attempted to monitor burrow temperature fluctuations in the field, but burrows are usually in the shade, with most eggs several centimetres below the mud surface, where they will be cooler than soil surface temperature. Because of the long-term nature of some of the experiments, some nests were brought to the laboratory in Glasgow, where they were maintained in an aquarium at an air temperature of 24-26°C. No attempt was made to regulate the lighting regime in either laboratory, since earlier experiments had shown that tadpoles make foam equally well in the dark and in the light (Downie, unpublished observations). There was no evidence that transportation of foam-making tadpoles to Glasgow caused any ill-effects.

Experiment 1: Growth to Metamorphosis

For this experiment, 20 foam nests were used, 8 in Trinidad and 12 in Glasgow. At intervals after collection (see Table 1 for times), 13 tadpoles were removed from each foam nest. Three of these were fixed in Bouin's fluid and later wet-weighed to 0.1 mg using a Sartorius Research balance: this established the state of the tadpoles at the start of the experiment. The remaining 10 tadpoles were transferred to 2 litre open polythene tubs containing 1500 ml dechlorinated copper-free tap water. Each tub was constantly aerated, and tadpoles were fed daily with crumbled fish flakes. The water was changed every 5-6 days. In Trinidad, water temperature was fairly constant at around 26°C, whereas in Glasgow it remained at 22-23°C.

Tadpoles were allowed to grow until they began to metamorphose, defined as the day of forelimb emergence (Gosner stage 42). On this day, metamorphosing tadpoles were wet-weighed to 0.01g. In the 1993 Glasgow series, after recording the wet weight at metamorphosis, tadpoles were fixed in Bouin's fluid. Snout-vent lengths were later measured to 0.1 mm using a binocular microscope and callipers. After this, tadpoles were dried in an oven at 80°C and dry weights were recorded to 0.1 mg. Lengths and dry weights were not measured in the 1991 experiment.

Time of death and approximate size were recorded for tadpoles that died during the experiment. These observations were not completely accurate because dead tadpoles were often consumed by the survivors.

The following data were recorded: proportion of tadpoles that reached metamorphosis; time taken to reach metamorphosis; and dry weight, wet weight, and length at metamorphosis.

Experiment 2: Short-term Growth Response

For this experiment, carried out in Trinidad (1993), six foam nests were used. At regular intervals after foam nest collection, samples of tadpoles were withdrawn as follows to assess their early response to growth conditions. For each foam nest, two 2 litre polythene tubs containing 1500 ml dechlorinated and aerated tap water were set up. To one tub, eight tadpoles were added and fed daily on crumbled fish flakes. Four tadpoles were removed and fixed in Bouin's fluid after one day, and the remainder after two days. To the other tub, 12 tadpoles were added but not fed. Four tadpoles were removed and fixed after 1, 2 and 6 days. In addition, on the day of setting up the tubs and six days later, four tadpoles were removed from the foam nests and fixed as controls. Laboratory air temperature was 28-29°C. Preserved tadpoles were later measured to 0.1 mm using an eyepiece graticule in a Wild M5 binocular microscope at X60 overall magnification; wet and dry weights were measured to 0.1 mg.

Histological Processing and Examination

Abnormal tadpoles were fixed in Bouin's fluid, embedded in paraffin wax, serially sectioned at 7 μm and stained with haemalum, eosin and alcian blue; they were examined with a Wild M20 microscope.

RESULTS

Growth to Metamorphosis

The aim of this experiment was to compare the ability to reach metamorphosis of tadpoles kept for different times in their foam nests. Time since egg deposition was known to 1-2 days for all foam nests used. The variable times since deposition used in the comparison differed for the Trinidad and Glasgow experiments because of collection and transportation requirements. In Trinidad, six of the foam nests used had tadpoles left after all growth experiments were set up: mean survival time post-deposition for these tadpoles was 17.5 days; in Glasgow, mean survival for seven nests of tadpoles was 32.4 days. In the Trinidad experiment, the longest time since deposition before tadpoles were set to grow was 17 days; in Glasgow, 32 days: the latter group was therefore close to the end of the survival capacity of these tadpoles in foam.

TABLE 1. Percentage of tadpoles reaching metamorphosis. Time class is the time between egg deposition and tadpoles entering water. *t*-test result given for Trinidad comparison; ANOVA performed for Glasgow comparison on arcsin-transformed percentages. ** $P < 0.01$. *Post-hoc* comparisons were C with D, E and F; D with E and F; E with F: superscripts which differ indicate significant differences between treatments ($P < 0.05$).

	Series	Time class (days) mean±SD	No. of group	% reaching metamorphosis Mean±SD	% reaching metamorphosis Range	Statistics
A	Trinidad	5.6±0.9	8	95.0±7.6	80 - 100	$t = 1.43$ NS
B		12.8±3.4	4	87.5±12.6	70 - 100	
C	Glasgow	9.9±3.0	9	96.7±5.0[a]	90 - 100	$F_{3,34} = 5.5$**
D		17.5±1.5	12	85.0±23.5[a]	20 - 100	
E		26.0±1.5	11	60.7±25.5[b]	0 - 90	
F		31.0±0.6	6	41.7±20.4[b]	10 - 70	

TABLE 2. Relationship between metamorphic potential and the condition of tadpoles in five foam nests. Metamorphic potential is given as the percentage of tadpoles reaching metamorphosis from an initial group of 10 (Column A). Tadpole condition is given as the mean wet weight (mg±SD) of a sample of 3-4 tadpoles taken from the nest at the same time as 10 tadpoles started growth to metamorphosis (Column B).

	Nest number									
	1		2		3		4		5	
Mean days since egg deposition	A	B	A	B	A	B	A	B	A	B
9.9	100	12.2±0.9	100	15.7±0.7	100	10.9±0.5	100	10.3±0.2	90	11.5 ±0.5
17.5	20	8.1±1.5	100	16.6±1.1	90	11.3±1.1	90	11.6±0.8	80	10.9±1.3
26.0	0	6.6±0.7	90	11.7±2.0	80	7.6±2.3	50	6.4±1.4	60	7.5±1.4
31.0	10	6.4±1.0	70	7.8±0.7	40	6.1±1.2	50	5.0±0.6	50	5.2±1.1

Proportion of tadpoles reaching metamorphosis. In both the Glasgow and the Trinidad series, there was a trend towards declining ability to reach metamorphosis the longer tadpoles remained in foam (Table 1). For tadpoles set up just after foam-making began, only seven out of 170 failed to reach metamorphosis; but tadpoles entering water about 30 days after egg deposition had less than a 50% chance of reaching metamorphosis. Observations on the time and stage of death showed no particular trend. Some died very small; others died near metamorphosis, and others in between. In most cases, there was no obvious cause of death. In a few, tadpole development was clearly abnormal: one had a twisted vertebral column and could not swim properly; in several, the body cavity became considerably distended, apparently full of air, and the tadpoles tended to swim sluggishly at the surface, before eventually dying. Histological examination of sections of such tadpoles showed a highly abnormal intestine, set to one side rather than filling the whole abdominal cavity and with a contracted lumen. Individual cells, however, looked healthy and the cause of this abnormality was not apparent.

The trend shown by the complete data set also occurred in individual foam nests. Results from 5 Glasgow nests are shown in Table 2. There was considerable variability between foam nests, with nest 1 showing a particularly steep decline in metamorphic potential, but nest 2 having high metamorphic potential even 31 days after deposition.

Table 2 also shows the mean wet weights of tadpoles taken from the foam nests at the times tadpoles were transferred to water to allow them to grow. For each nest, wet weight declined the longer tadpoles remained in foam, but the rate of decline differed from nest to nest: it was steepest for nest 1, correlating with the steepness of decline of metamorphic potential in this nest and shallowest for nest 2, which had the longest duration of high metamorphic potential. The remaining three nests were intermediate between these extremes in both weight and metamorphic potential decline.

Time taken to reach metamorphosis. The data on time taken to reach metamorphosis are shown (Table 3) as (1) time taken for the first tadpoles to reach metamorphosis, (2) time between the first and last metamorphosis - a measure of whether all tadpoles in a

TABLE 3. Time (days) taken by tadpoles to reach metamorphosis after being put in water with food: (a) time taken for the first tadpole in each group to reach metamorphosis; (b) time between first and last metamorphosis in a group; (c) time for all tadpoles in a group to reach metamorphosis. Superscript 1 denotes data sets where the percentage of tadpoles reaching metamorphosis was sometimes less than 80%. Figures in brackets show the data for those cases where 80% or above did metamorphose. t-test results given for Trinidad comparisons. ANOVA results given for Glasgow comparisons. $*P < 0.05$; $**P < 0.01$. *Post-hoc* comparisons were C with D, E and F; D with E and F; E with F. Superscripts which differ indicate significant differences between treatments ($P < 0.05$).

		Series	Mean days since egg deposition	No. of groups	No. days (mean±SD)	Statistics
(a)	A	Trinidad	5.6	9	16.8±3.2	$t = 0.51$ NS
	B		12.8	7	16.0±2.6	
	C	Glasgow	9.9	9	$18.6±2.9^a$	
	D		17.5	13	$29.5±9.7^b$	$F_{3,34} = 4.39*$
	E		26.0	10	$29.5±9.2^b$	
	F		31.0	6	$32.8±12.1^b$	
(b)	A	Trinidad	5.6	8	8.0±3.8	$t = 0.79$ NS
	B		12.8	3	6.0±2.0	
	C	Glasgow	9.9	9	$14.2±8.6^a$	
	D		17.5^1	12	$42.0±19.9^b$	
				(10)	(47.2±17.4)	$F_{3,32} = 8.05$
	E		26.0^1	10	$41.8±15.0^b$	
				(4)	(45.3±18.0)	
	F		31.0^1	5	$57.6±22.2^b$	
				(0)		
(c)	A	Trinidad	5.6	8	19.6±4.1	$t = 1.27$ NS
	B		12.8^1	4	16.7±2.4	
				(3)	(17.2±2.9)	
	C	Glasgow	9.9	9	$24.3±6.9^a$	
	D		17.5^1	12	$46.5±12.1^b$	
				(10)	(47.6±11.8)	$F_{3,32} = 3.45*$
	E		26.0^1	10	$48.2±12.2^b$	
				(4)	(42.0±10.0)	
	F		31.0^1	5	$61.1±22.2^b$	
				(0)		

group developed together, or whether they were very spread out, and (3) mean time for all to reach metamorphosis: since a high proportion of tadpoles in the higher time classes failed to reach metamorphosis, these data are presented in two ways - mean times for all that metamorphosed, and mean times for groups where 80% or more did metamorphose.

The minimum time taken for any tadpole to reach metamorphosis was 12 days (17 days after egg deposition) and the maximum recorded was 143 days (including 32 days in foam, this was 175 days after egg deposition). Inspection of Table 3 shows that the longer tadpoles remained in foam, the longer it took to reach metamorphosis, whether the measure was of the first tadpole to reach metamorphosis, or the mean time for all tadpoles. The discrepancy concerns the two Trinidad groups where times to metamorphosis are not distinguishable. Compared to the Glasgow groups, all the Trinidad tadpoles had been kept in foam for a relatively short time.

FIG. 1. Group of 10 tadpoles from a single clutch grown for 36 days, after 20 days kept in a foam nest. The largest in the group is near metamorphosis; the smallest has hardly grown at all. Scale bar = 20 mm.

TABLE 4. Mean wet weights, in grams, for all tadpoles in each group, on reaching metamorphosis. Superscript 1 denotes data sets where the proportion of tadpoles reaching metamorphosis was sometimes less than 80%. Figures in brackets show the results for those cases where 80% or above did metamorphose. t - test results given for Trinidad comparisons. ANOVA results given for Glasgow comparisons. $*P < 0.05$. *Post-hoc* comparisons were C with D, E and F; D with E and F; E with F. Superscripts which differ indicate significant differences between treatments ($P < 0.05$), except mean wet weights D and E NS.

	Series	Mean days since egg deposition	No. of groups	Mean wet wt.±SD	Statistics	Mean std. dev. ±SD	Statistics
A	Trinidad	5.6[1]	9	0.24±0.04	$t = 0.014$ NS	0.04±0.01	$t = 0.49$ NS
			(8)	(0.25±0.04)		(0.04±0.01)	
B		12.8[1]	5	0.24±0.04		0.04±0.02	
			(3)	(0.24±0.04)		(0.03±0.01)	
C	Glasgow	9.9	9	0.25±0.02[a]	$F_{3,32} = 4.75*$	0.03±0.0[1a]	$F_{3,32} = 4.74*$
D		17.5[1]	12	0.29±0.03[a]		0.08±0.03[b]	
			(10)	(0.29±0.03)		(0.08±0.03)	
E		26.0[1]	10	0.32±0.08[b]		0.08±0.03[b]	
			(4)	(0.28±0.02)		(0.08±0.02)	
F		31.0[1]	5	0.37± 0.10[b]		0.12±0.10[b]	
			(0)				

TABLE 5. Mean dry weight (mg) for all tadpoles in each group, on reaching metamorphosis (measured only in Glasgow, 1993 experiment). Superscript 1 denotes data sets where the proportion of tadpoles reaching metamorphosis was sometimes less than 80%. Figures in brackets show the results for those cases where 80% or above did metamorphose. Means compared by ANOVA. $**P < 0.01$. *Post-hoc* comparisons were A with B, C and D; B with C and D; C with D. Superscripts which differ indicate significant differences between treatments ($P < 0.05$).

	Mean days since egg deposition	No. of groups	Mean dry wt. ±SD	Statistics	Mean std. dev. ±SD	Statistics
A	9.9	7	37.5±3.9[a]	$F_{3,24} = 6.83**$	5.2 ±1.4[a]	$F_{3,24} = 14.94**$
B	17.5[1]	10	48.7±6.0[b]		16.0± 5.4[b]	
		(9)	(47.7±5.4)		(17.0±4.7)	
C	26.0[1]	6	53.2±8.6[b]		13.9±2.9[b]	
		(3)	(47.1±5.3)		(14.8±3.7)	
D	31.0[1]	5	(54.4±11.9[a])		12.5±4.9	

As expected from the laboratory temperature differences, all times in Glasgow were somewhat longer than in Trinidad. In addition, the longer tadpoles remained in the nest, the more variable was their time to reach metamorphosis, measured both by the time between first and last metamorphosis and by the standard deviations of the mean times. One group set up soon after egg deposition all metamorphosed over two days, whereas it took 95 days from the first to last in one group set up after 31 days in the nest.

This variability is evident in Fig. 1, a photograph of a complete group of tadpoles set up after 26 days in the nest, just as the first tadpole was beginning to metamorphose after 36 days in water with food. The smallest tadpole here was hardly bigger than when it was removed from the foam nest. Only three of this group eventually reached metamorphosis.

Sizes of tadpoles on reaching metamorphosis. The sizes of tadpoles at metamorphosis were measured in three ways: snout-vent length (not shown), wet weight (Table 4), and dry weight (Table 5). As with the time-to-metamorphosis results, there was no significant difference between the two Trinidad groups. However, in the Glasgow experiments, all measures of size at metamorphosis showed that size was greater the longer the time tadpoles had spent in the nest. In addition, variation in size at metamorphosis also increased with time in the nest. For example, from one foam nest, dry weights at metamorphosis changed from 35-48 mg (mean=40, n=9) for the group earliest out of the nest to 45-96 (mean=61, n=6) for the group last out of the nest. That size at metamorphosis should increase the longer tadpoles remained in the foam nest was a totally unexpected result.

TABLE 6. Rate of growth to metamorphosis measured as dry weight (mg) at metamorphosis, divided by the number of days taken to reach metamorphosis after access to food. Superscript 1 denotes data sets where the proportion of tadpoles reaching metamorphosis was sometimes less than 80%. Figures in brackets show the results for those cases where 80% or above did metamorphose. Means compared by ANOVA. NS $P > 0.05$.

Mean days since egg deposition	No. of groups	Mean dry wt./day ±SD	Statistics
9.9	7	1.60±0.32	$F_{3,24}$= 2.49 NS
17.5[1]	10 (9)	1.16±0.37 (1.07±0.25)	
26.0[1]	6	1.27±0.43 (1.27±0.62)	
31.0[1]	5 (0)	1.01±0.53	

Rate of growth of tadpoles in reaching metamorphosis. Table 6 gives the rate of growth to metamorphosis in terms of dry weight gain per day for the different groups, using only data from the Glasgow 1993 experiment. The results show that the longer tadpoles remained in foam, the slower they grew once they were given access to water and food.

SHORT-TERM GROWTH RESPONSE

The results of the short-term growth experiments (Table 7) are based on pooled data from six different nests. Tadpoles in foam nests declined gradually and continuously in dry weight over the 31 day period monitored after egg deposition, ending at 38% of starting weight.

When added to water with food, tadpoles grew rapidly, but the rate of growth varied according to the length of time spent in the foam nests. Intriguingly, the fastest growth in dry weight was not in the earliest group (= 5 days after egg deposition) but in the second group (= 15 days); and in the third group (= 25 days) growth rate, both in percentage terms and absolute terms (amount of dry mass added per day), was similar to the earliest group. After two days growth, tadpoles in the third group were smaller than the others, but they started from a lower initial weight. Wet weight and length measurements (not shown) showed essentially the same pattern of changes. It should be noted that not all the growth recorded is tissue growth: for these tadpoles, unassimilated food in the gut is a significant proportion of body weight.

When added to water with no food, to test the effect of tissue hydration alone, there was no significant change in dry weight in any group of tadpoles. However, in the earlier groups, body length and wet weight did increase continuously over the six days in water. In the third group there was an initial increase in wet weight and body length over the first day but no increase over the following five days.

DISCUSSION

Body condition of *Leptodactylus fuscus* tadpoles kept in their foam nests for progressively longer periods was investigated. Previous work (Downie, 1994*a*) established that tadpole weight declined the longer tadpoles remained in the nest and that they eventually died if they did not get access to food and water. Mean survival time post-deposition was 27.5 days (range 19-33; 6 nests). In the present study, mean survival time was 32.4±2.7 days (range 27-36; 7 nests; maintained in

TABLE 7. Short term growth response: dry weight measurements (mg; mean ± SD; number sampled in brackets). ANOVA results given for each group.*** $P < 0.001$. *Post-hoc* comparisons were A with B, C and D. B with C and D. Superscripts which differ indicate significant differences between treatments ($P< 0.05$).

Group	Days since egg deposition (mean±SD)	Tadpoles taken from foam nest (controls)		Tadpoles in water with no food			Tadpoles in water with food		Statistics
		Day 0 A	Day 6	Day 1 B	Day 2	Day 6 C	Day 1 D	Day 2	
1	5.3±0.8	2.1±0.5[a] (25)	1.9±0.4 (18)	2.3±0.4[a] (24)	2.4±0.7 (23)	2.2 ± 0.6[a] (25)	3.2±0.5[b] (24)	5.6±0.8 (24)	$F_{6,157}$= 21.2***
2	15.3±0.8	1.5± 0.4[a] (22)	1.4±0.4 (17)	1.6± 0.3[a] (18)	1.6± 0.4 (19)	1.7±0.7[a] (15)	3.9 ± 0.6[b] (22)	6.9±1.8 (22)	$F_{6,129}$=123.2***
3	25.3±0.8	1.0±0.3[a] (21)	0.8±0.3 (23)	1.3±0.3[a] (21)	1.2 ± 0.3 (19)	1.0± 0.4[a] (17)	2.0±0.5[b] (22)	3.9±1.0 (22)	$F_{6,139}$=92.9***

Glasgow). The longer survival time may partly be explained by lower maintenance temperature, and partly by improved husbandry of the foam nests. The results reported here extend the earlier work to include a study of the responses of tadpoles given access to water and food after different times in the nest.

The longer tadpoles remained in their foam-nests, the less likely they were to reach metamorphosis, the longer it would take on average, and the slower they would grow. Within these broad trends were three more surprising findings. First, decline in metamorphic potential varied considerably from clutch to clutch. Second, within any one clutch, the longer tadpoles remained in foam, the more variable their metamorphic potential became. Third, the longer tadpoles remained in foam, the larger their mean size at metamorphosis became.

The second response measured was initial growth rate, for the period 1-6 days after tadpoles were given access to water and food. In water alone, no increases in dry weight occurred, but length and wet weight measurements revealed a difference in response according to the time spent in the foam nest. Tadpoles kept in foam up to 15 days after egg deposition retain some yolk reserves (Downie, 1994*a*) and in water alone, these tadpoles grew in body length and wet weight for the six days of the experiment, presumably converting the yolk into tissue, especially gut. Tadpoles kept in foam 25 days had no yolk left, and these tadpoles merely showed a one-day increase due to tissue hydration.

When tadpoles were given food, all growth measurements showed increases over two days, but rates differed according to time spent in foam. The fastest growth occurred 15 days after egg deposition with the rate being slower at five and 25 days. The most likely explanation of these results is that at five days, the food gathering and processing system is still relatively immature. Tadpoles are able to gather and utilize food, but not quite so effectively as somewhat older tadpoles. However, by 25 days, body weight has begun to decline, involving tissue breakdown to provide for metabolic needs: this may lead to a progressive decline in the effectiveness of food gathering and processing.

The most general result from this study is that the longer tadpoles remained in foam, the less likely they were to reach metamorphosis once they had access to food and water. In other words, they had declined in some manner in body condition. Part of the reason for this may be the decline in body weight experienced by tadpoles towards the end of the foam-making period. However, tadpoles at this stage given food and water were able to grow and in most clutches, some eventually reached metamorphosis, so the growth decline did not in itself mean that tadpoles were doomed to die. A possible additional factor contributing to the decline in metamorphic potential is infection: during the time in foam, various kinds of micro-organisms may become associated with the tadpoles and cumulatively lead to deterioration in physiological systems. Downie (1994*a*) noticed that the guts of tadpoles in foam contained large numbers of unicellular organisms; and tadpoles that died at various times after entering water often showed signs of fungal attack. There has been considerable controversy over the identity of the unicellular organisms commonly found in tadpole guts and over their role in the phenomenon of competitive growth inhibition (Beebee, 1995; Petranka, 1995) but their effects on non-growing tadpoles in foam nests are unknown.

There is now a considerable literature on the plasticity of tadpole development, based on the suggestion by Wilbur & Collins (1973) that many tadpole species may respond adaptively to their recent growth history - metamorphosing if this is slow, remaining to grow further in water if fast. Results from different studies have been variable, one showing the prime determining factor as early food supply (Leips & Travis, 1994), another that growth rate in the middle period is the main determinant (Hensley, 1993). In some cases, plasticity appears not to be adaptive (Tejedo & Reques, 1994); in others, as in a series of studies on the desert amphibian *Scaphiopus couchii* (Newman 1988, 1989, 1994), a clearly adaptive response to food, water and space has been demonstrated. These studies have all been on tadpole species that begin feeding immediately. The situation described here for *Leptodactylus fuscus*, with tadpoles remaining up to several weeks in the nest before starting to feed, is highly unusual. However, this factor - time in the nest before feeding - had an effect on future development under constant conditions: the longer the time in the nest, the longer the growth period, the larger the mean size at metamorphosis, and the more variable the time to, and size at, metamorphosis. Another variable was the speed of change in body condition which differed greatly from clutch to clutch.

Are any of these effects adaptive? We doubt that this question can be answered fully at present. However, knowledge is accumulating of unexpected adaptive responses to unpredictable environments and it is not unreasonable to suggest that for *L. fuscus* tadpoles that enter water early, the adaptive response is to regard conditions as generally good, allowing uniform growth to optimal size; but for those that remain longer and longer in foam, conditions may be perceived as patchy, encouraging something like a 'coin-flipping' response (Kaplan & Cooper, 1984) where some individuals choose rapid development to early, small size metamorphosis and others choose late, large size.

Another possibility worth investigating in this system is polyphenism. Pfennig (1992) found that *Scaphiopus multiplicatus* tadpoles develop as large carnivorous morphs or smaller omnivorous morphs, depending on resource availability and quality. The body shape of the large *L. fuscus* tadpoles reported here is similar to Pfennig's carnivores, while the smaller *L. fuscus* are like the omnivores. Again, the extremes of size in *L. fuscus* developed in response to longer peri-

ods of developmental arrest in foam, and could therefore involve some kind of developmental switch. Testing whether the proportion of large to small morphs is responsive to conditions and whether the two morphs differ in features other than size (as do the *S. multiplicatus* morphs) will be an objective of future research.

Although some of the life history features revealed by this study may be adaptive, the main result is the decline in metamorphic potential the longer tadpoles remained in the foam nest. It is possible that the results are partly artefactual: foam nests were maintained on damp tissue, rather than on mud; tadpoles were kept in aquaria and fed artificially. It will therefore be worth attempting to replicate this work under more natural conditions. If the results do reflect reality in the field, decline in tadpole condition and metamorphic potential must be a limitation on the success of the *L. fuscus* strategy of reproducing in advance of major rainfall. The magnitude on this limitation will vary with rainfall patterns.

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PHYLOGENETIC RELATIONSHIPS AMONG AUSTRALIAN ELAPID SNAKES: THE SOFT ANATOMICAL DATA RECONSIDERED

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On the basis of an extensive set of visceral and scale characters, Wallach (1985) proposed a detailed phylogenetic scheme for all the Australian elapids, down to species level. The shortest tree found in that analysis is here shown to contain 592 steps. However, a re-analysis of the same data using PAUP 3.1.1 reveals that there are 258 most parsimonious trees, each with only 578 steps. The strict consensus of these trees is much less resolved than Wallach's tree, and has a different topology. For example, *Echiopsis* is most closely related to *Suta fasciata* rather than to the *Notechis* lineage, and *Demansia* is more closely related to advanced elapids (such as the *Notechis* lineage) than to *Oxyuranus* and *Pseudonaja*. Many of the larger (suprageneric) groupings proposed by Wallach are paraphyletic in the PAUP consensus tree. Almost all the groupings in this tree, however, can be collapsed with the addition of a single extra step. There are more than 32 000 cladograms at 579 steps, one step longer than the 258 most parsimonious cladograms. A strict consensus tree of cladograms 578 and 579 steps long is almost completely unresolved. The visceral and external morphological traits, therefore, are not as phylogenetically informative as previously proposed, at least with respect to the Australian elapid radiation. These types of characters might not be very phylogenetically informative at higher (intergeneric) levels, although much more data are required to test this hypothesis.

INTRODUCTION

Elapid (proteroglyphous) snakes have undergone a rapid and diverse adaptive radiation in Australia, and form the largest single component (approximately half) of the continent's snake fauna (e.g. Shine, 1985). This contrasts strongly with the snake faunas of other continents, which are dominated by colubrids. The Australian elapid radiation therefore represents an unusual and intriguing evolutionary event. However, phylogenetic relationships among these snakes have been subjected to few detailed studies and are still rather poorly known.

The only studies of Australian elapid phylogeny which sampled a broad range of taxa and characters were published together in a symposium volume. Schwaner et al. (1985) used immunological distances, Mengden (1985) used electrophoretic and chromosomal traits, and Wallach (1985) considered internal soft anatomical (visceral) and external (scale) characters. Of these studies, Wallach's data set was by far the most extensive in terms of number of characters and number of taxa sampled. It was also the only study that adopted an explicitly cladistic approach. Wallach's conclusions have resulted in taxonomic changes (e.g. Hutchinson, 1990) and have been used, along with other studies (e.g. Mengden, 1985), as the basis for ecological inferences (e.g. Shine, 1985, 1994). It is therefore important that the study is critically evaluated.

Because of the size of Wallach's data matrix, the parsimony programs available at the time could not evaluate it effectively. Analysis of the same data set using PAUP 3.1.1 (Swofford 1993), shows that the most parsimonious trees are very different to the tree proposed in Wallach (1985), and further shows that the phylogenetic signal is extremely weak. Also, some ambiguities regarding character codings in Wallach's data set are clarified.

THE DATA SET

Wallach's data matrix (his Appendix C) is reproduced here as Table 1. In Wallach's matrix, taxa were ordered, not by genera, but alphabetically by specific name (the second part of the binomial). Thus, species of different genera were shuffled together. Here, the species have been grouped according to genera, and similar genera also grouped together, making visual comparisons of character states in similar taxa easier.

In Wallach's study, 63 species of Australian elapids were examined, representing all recognized genera and the majority of recognized species. 50 potentially informative characters were identified, mostly involving the viscera and external morphology. These characters were polarized by outgroup comparison, using chiefly the African elapid *Naja melanoleuca*. Myological characters were not used, nor were skeletal characters, apart from tooth counts.

However, in Wallach's data matrix there were 72 characters. This discrepancy was not explained, and several colleagues (e.g. Scanlon pers. comm., Shea pers. comm.) have had problems interpreting this matrix. The reason for this discrepancy is that Wallach ordered his multistate characters into morphoclines (Wilkinson, 1992; Slowinski, 1993). Multistate characters that formed bifurcating series (i.e. two divergent morphoclines from the primitive condition) were recoded as two separate characters, one for each morphocline. This procedure is discussed in Wiley *et al.* (1991). There were 22 such characters in the 50

TABLE 1. The computer data matrix of Wallach (1985). The order of taxa has been modified so that species are grouped according to genera, and similar genera have been grouped together. The 72 characters are discussed in the text. The correspondence between the 72 characters in Wallach's computer data matrix (Appendix C), and the 50 characters in Wallach's text and Appendix B, is shown in the top two rows.

CHARACTERS (APP. C)	123456789111111111222222222233333333334444444444555555555566666666667777 012345678901234567890123456789012345678901234567890123456789012345678901234567890123456789012
CHARACTERS (APP. B & TEXT)	<1<2<3<4<5<6<78911111<1<1<1<1<11<2<2<222<2<2<222333333<3333444<44<4<44<445 01234 5 6 7 89 0 1 234 5 6 789012345 6789012 34 5 67 890
Outgroup (Naja melanoleuca)	00000000000000000000000000000000000000000000000000000000000000000000000000000000000000
Demansia atra	00000001001010000010101000000000000011011000000001000002100010120022012 0
Demansia olivacea	00000000011000100000001000000000000011001010100001000002100010120002012 0
Demansia psammophis	00000000011000101100000000000000010001100101000000100000210001012000201 20
Demansia torquata	00000000001001101111101000000000100000001010100001011002100010120002012 0
Pseudechis australis	00000000100000100000000101000100000000000000000001000001110100110001002 1
Pseudechis guttatus	00000001000000000000001000000000000011000000000001000000111001100010020
Pseudechis porphyriacus	00100100101010000100000010110010001000000000000001000001110100110001002 1
Oxyuranus microlepidotus	10001010001001100000000000010001001001100001000001101000002000101001012 0
Oxyuranus scutellatus	10001010001000101000100000000010010011000000001011100000020011010020120
Pseudonaja affinis A	10001010011000120000000000000001001000000000011001100000010001010000101 20
Pseudonaja affinis B	10001010101000101101000001000001001010000000011001101100000001010000101 20
Pseudonaja guttata	10001010000000101010001010000001001001000000011001110000010001000000101 20
Pseudonaja modesta	00000000010000101111100101001000110100101001100110000011000101000110110
Pseudonaja nuchalis	10101010001000100000100000000001001000000000010011001000100010100001012 0
Pseudonaja textilis	10001010000001101001101000000001101011000000010011000001111010100001012 0
Acanthophis antarcticus	01000101001000100000210010110101101000010100110100011010011001101000102 1
Acanthophis pyrrhus	00000000000001121101200000010101101000010100110101000010010000001000102 1
Austrelaps superbus	00000001000001000000101000010100001000010100000001000002020010110001102 1
Notechis scutatus	10001000000000110000201000010100001001010100000001000000200001010011021
Notechis ater	00000010011010000010001010110100001000010100100001000000200001010011021
Tropidechis carinatus	10001000011010000010001100000100001000010100110100000000021000101101011 1
Hoplocephalus bitorquatus	00000000000000010000010110000010001000000000110002100000002000000120001 01
Hoplocephalus bungaroides	10001010011010000010001000010100001001000101100021000000020000001100010 1
Hoplocephalus stephensii	00001000001000000110000100000100001000100001100021000000021000001200010 1
Denisonia maculata	01000101011001100110100000000101000000010101200001000001020000001011100 1
Denisonia devisii	01010101010000100100200000010111001000000101011000010000010200000010111001
Hemiaspis damelii	00000000011001100000101000010110000001010100100001001001120010120011001 1
Hemiaspis signata	00000101010000100100201100000110010000010100100001000001120010120011001 1
Echiopsis curtus	10001010010000020110200000000101000000010101100000100010120000101001101 1
Suta fasciata	10011010011010121010200101000101010000010101100001100001020000110011100 1
Suta flagellum	00010000011010121111210001000101011000010100200001000001020000110010000 1
Suta gouldii	00000000010101121111200101000101000011010101100001100102020000110010000 1
Suta monachus	00000000011000121111100001000101000100010101210001000002020000110010000 1
Suta nigriceps	00000000010100101000210000000101001010010101100001000002020000110010000 1
Suta punctata	00000000011000121100200000000101101011010101200001000002020000110011100 1
Suta suta	00010000010000101111100000000101000000010101100001100000020000110010000 1
Drysdalia coronata	00000000011000100100000000000101000000010100200001000002020000101011001 1
Drysdalia coronoides	01000001010000100110100100000100000001010111020000000002120000100011001 1
Drysdalia mastersii	01000101100000100110201000100100000000010100200001000002020000100011001 1
Drysdalia rhodogaster	00100100010000000100010100000100000000010110200001000002020000100011001 1
Rhinoplocephalus bicolor	10100000010001000010201101000100100010010101201001010002020000120011000 1
Rhinoplocephalus boschmai	00000000010000000100100000000101001000010101200001100002020000110010000 1
Rhinoplocephalus nigrescens	00001000010001100100101101000101000000000101100001000002120000100012000 1
Rhinoplocephalus nigrostriat.	00000001001001110000201000000101000000010010100001010002020000110010000 1
Rhinoplocephalus pallidiceps	00000001010100000100001100000101001001010101210001000002020000100011000 1
Elapognathus minor	00000001010001000100201000110100001000010010200001000002020001100011000 1

TABLE 1. (continued...)

Cacophis harriettae	0100010101000012110100010000010101000001010121000110000210011010001000000
Cacophis krefftii	0000000001100012110110010000110100000101010121000100000210010110001000000
Cacophis squamulosus	0100010100000110110100000001010100000101010111000100000210011010001000000
Furina barnardi	0000000001100110011021000100110100000001010121000010000210000000001000000
Furina diadema	0000000001001000011020010000010101000001010121000010000210010000001000000
Furina dunmalli	0100010001010110010000000000010100100001010110000110000010001000001000000
Furina ornata	0000000001100012110100000100110100000100000020000110000100010000001000000
Furina tristis	0101010000100012010001000000010110100001010010000110000111010000001000000
Simoselaps australis	1001100010101002010000110100010100001001010121000100000111000100002000000
Simoselaps bertholdi	0100010101010112011000100001010101001001010121000100000210000100002000000
Simoselaps bimaculatus	1000101001000110011000110100110100011000010121000200000210010100001000000
Simoselaps calanotus	0010010101000110011000110100010110001001010121000100000210010100001000000
Simoselaps fasciolatus	0001000100000112011000110000010100000001010121000110010111000010000200000
Simoselaps roperi	0010010001000012010020010100110100001001010121000200010210010100002000000
Simoselaps semifasciatus	0000010101000112111110010100010100101001010121000100000110010100002000000
Simoselaps warro	1010001001100002000020000100010110100001010121000110000210000000001000000
Vermicella annulata	1000101001000010011020010100110100011000010111100200000210010100002001000

characters described in the text. These 22 characters were each re-coded as two characters in the data matrix (Appendix C), giving a total of 72 characters.

The definitions for the character states for the 72 re-coded characters were not listed. However, they can be inferred by comparing the original descriptions for the 50 characters with the data matrix. The order of characters was kept the same in both; however, as bifurcating characters in the descriptions were each re-coded as two characters in the computer matrix, the numbering sequence was different. The correspondence between the two sets of characters is shown in Table 1. Inspection of the data matrix, and comparisons with specimens, revealed that, where bifurcating characters were re-coded as two characters, usually the first of the re-coded characters corresponded to the *second* direction of change mentioned in the character description, and the second re-coded character to the *first* direction of change. For instance, character 1 in the descriptions (ratio of right lung length to snout-vent length) is bifurcating and was re-coded as two characters. The morphoclines mentioned in the description are: low (0.311-0.422), intermediate (0.423-0.519) and high (0.52-0.74). Thus, the first of the recoded characters (character 1 in the matrix, see Table 1) refers to the presence/absence of the second change, towards the derived state of a high ratio: i.e. primitive (0), ratio 0.519 or less; derived (1), ratio 0.52 or more. The second of the re-coded characters (character 2 in the matrix, see Table 1) refers to the presence/absence of the first change, towards the derived state of a low ratio: i.e. primitive (0), ratio 0.423 or greater; derived (1), ratio 0.422 or less.

Because the alternative character states for the 72 recoded characters were not stated by Wallach, and have posed some problems for other workers, they are listed below. The original numbering system in the text (50 characters) is shown in brackets after each character number. However, the details of each measurement (e.g. how each ratio is calculated) were clearly discussed by Wallach, and thus are not repeated.

1 (1a). Right lung / snout-vent ratio. 0.519 or less, 0. 0.52 or more, 1.

2 (1b). Right lung / snout-vent ratio. 0.423 or more, 0. 0.422 or less, 1.

3 (2a). Vascular portion of right lung / snout-vent ratio. 0.112 or more, 0. 0.111 or less, 1.

4 (2b). Vascular portion of right lung / snout-vent ratio. 0.16 or less, 0. 0.161 or more, 1.

5 (3a). Avascular portion of right lung / snout-vent ratio. 0.374 or less, 0. 0.375 or more, 1.

6 (3b). Avascular portion of right lung / snout-vent ratio. 0.296 or more, 0. 0.295 or less, 1.

7 (4a). Position of caudal tip of right lung along snout-vent axis, measured as the ratio - snout to tip of right lung / snout-vent length. 0.763 or less, 0. 0.764 or more, 1.

8 (4b). Position of caudal tip of right lung along snout-vent axis, measured as the ratio - snout to tip of right lung / snout-vent length. 0.674, 0. 0.673 or less, 1.

9 (5a). Ratio of dense to spare parenchyma on right lung. 5 or less, 0. 5.1 or more, 1.

10 (5b). Ratio of dense to spare parenchyma on right lung. 2.5 or more, 0. 2.4 or less, 1.

11 (6a). Lung diameter / coelom diameter ratio. 0.75 or less, 0. 0.8 or more, 1.

12 (6b). Lung diameter / coelom diameter ratio. 0.5 or more, 0. 0.4 or less, 1.

13 (7a). Tracheal membrane / tracheal ring ratio. 1.9 or less, 0. 2 or more, 1.

14 (7b). Tracheal membrane / tracheal ring ratio. 1 or more, 0. 0.9 or less, 1.

15 (8). Left lung / snout-vent ratio. 0.01 or more, 0. 0.009 or less, 1.

16 (9). Tracheal entry. Subterminal, 0. Paraterminal or quasiterminal, 1. Terminal, 2.

17 (10). Left lung. Present, 0. Absent, 1.

18 (11). Left bronchus. Present, 0. Absent, 1.

19 (12). Free tips on tracheal rings. Absent, 0. Present, 1.
20 (13). Orifice for left lung. Present, 0. Absent, 1.
21 (14). Tracheal lung. Absent, 0. Small, 1. Moderate, 2.
22 (15a). Snout-heart / snout-vent ratio. 0.277 or less, 0. 0.278 or more, 1.
23 (15b). Snout-heart / snout-vent ratio. 0.233 or more, 0. 0.232 or less, 1.
24 (16a). Liver length / snout-vent ratio. 0.265 or less, 0. 0.266 or more, 1.
25 (16b). Liver length / snout-vent ratio. 0.212 or more, 0. 0.211 or less, 1.
26 (17a). Liver-gall bladder distance / snout-vent ratio. 0.398 or less, 0.399 or more, 1.
27 (17b). Liver-gall bladder distance / snout-vent ratio. 0.306 or more, 0. 0.305 or less, 1.
28 (18a). Kidney-vent distance / snout-vent ratio. 0.184 or less, 0. 0.185 or more, 1.
29 (18b). Kidney-vent distance / snout-vent ratio. 0.132 or more, 0. 0.131 or less, 1.
30 (19). Hyoid length / snout-vent ratio. 0.096 or less, 0. 0.097 or more, 1.
31 (20a). Position of umbilicus. Number of ventrals from umbilical to preanal scute / total number of ventrals. 0.187 or less, 0. 0.188 or more, 1.
32 (20b). Position of umbilicus. Number of ventrals from umbilical to preanal scute / total number of ventrals. 0.142 or more, 0. O.141 or less, 1.
33 (21a). Heart-liver distance / snout-vent ratio. 0.076 or less, 0. 0.077 or more, 1.
34 (21b). Heart-liver distance / snout-vent ratio. 0.048 or more, 0. 0.047 or less, 1.
35 (22a). Total kidney length (right plus left) / snout-vent ratio. 0.137 or less, 0. 0.138 or more, 1.
36 (22b). Total kidney length (right plus left) / snout-vent ratio. 0.085 or more, 0. 0.084 or less, 1.
37 (23). Distance between systemic arch junction and heart apex / snout-vent ratio. 0.01 or more, 0. 0.009 or less, 0.
38 (24). Diameter of right systemic arch / diameter of left systemic arch. 0.5 or more, 0. 0.4 or less, 1.
39 (25a). Number of ventral scutes. 228 or fewer, 0. 229 or more, 1.
40 (25b). Number of ventral scutes. 192 or more, 0. 191 or fewer, 1.
41 (26a). Number of subcaudal scales. 74 or fewer, 0. 75 or more, 1.
42 (26b). Number of subcaudal scales. 54 or more, 0. 53 or fewer, 1.
43 (27a). Tail length / total length ratio. 0.2 or less, 0. 0.21 or more, 1.
44 (27b). Tail length / total length ratio. 0.15 or more, 0. 0.14 or less, 1.
45 (28). Maximum total length. 1500 mm or more, 0. 1499 mm-600 mm, 1. 599 mm or less, 2.
46 (29). Temporolabial scale. Present, 0. Absent, 1.
47 (30). Internasal scale. Paired, 0. Fused, 1.
48 (31). Dorsal scales. Without carinae, 0. With carinae, 1.
49 (32). Ventral scales. Without keels, 0. Weakly keeled, 1. Strongly keeled and notched, 2.
50 (33). Number of supralabials. Seven, 0. Six, 1. Five, 2.
51 (34). Nasal-preocular contact. Present, 0. Absent, 1.
52 (35). Preocular scales. One, 0. Two, 1.
53 (36a). Postocular scales. Two or one, 0. Three, 1.
54 (36b). Postocular scales. Two or three, 0. One, 1.
55 (37). Subocular scales. Absent, 0. Present, 1.
56 (38). Mid-body dorsal scale rows. 23-19, 0. 17, 1. 15, 2.
57 (39). Anal plate. Single, 0. Divided, 1.
58 (40). Subcaudal scales. All paired, 0. Both paired and single, 1. All single, 2.
59 (41). Prey. All ectotherms, 0. 25-50% endotherms, 1. All endotherms, 2.
60 (42). Posterior scale row reduction. Present, 0. Absent, 1.
61 (43a). Maxillary teeth. Seven or fewer, 0. Eight or more, 1.
62 (43b). Maxillary teeth. Three or more, 0. Two or fewer, 1.
63 (44). Hemipenis. Forked, spinose, 0. Single, calyculate, 1.
64 (45a). Venom gland musculature. *Glyphodon* or *Oxyuranus* type, 0. *Pseudechis* type, 1. *Demansia* type, 2. This character refers to presence of the *Pseudechis* or *Demansia* type of musculature.
65 (45b). Venom gland musculature. *Glyphodon,. Pseudechis,* or *Demansia* type, 0. *Oxyuranus* type, 1. This character refers to presence of the *Oxyuranus* type of musculature.
66 (46a). Ecology. Terrestrial, sub-fossorial, or fossorial, 0. Semi-arboreal, 1. Arboreal, 2.
67 (46b). Ecology. Terrestrial, semi-arboreal, or arboreal, 0. Sub-fossorial, 1. Fossorial, 2.
68 (47). Sexual dimorphism. Females larger, 0. No dimorphism, 1. Males larger, 2.
69 (48a). Body shape. Moderate or thin, 0. Thick, 1.
70 (48b). Body shape. Moderate or thick, 0. Thin, 1.
71 (49). Circadian activity. Nocturnal, 0. Crepuscular, 1. Diurnal, 2.
72 (50). Reproduction. Oviparous, 0. Viviparous, 1.

Wallach (1985) analysed the data set using three different algorithms of the PHYSYS program (see Wallach, 1985 for full details). Multistate characters were ordered in all three analyses, and each character state change was given a weighting of one. The "Wagner" and "Pimentel" algorithms were alternative methods that attempted to find the most parsimonious tree(s), assuming characters were reversible. The WISS algorithm attempted to find the most parsimonious tree, under the assumption of irreversibility. The three trees found in these analyses are shown in Fig. 1.

I re-analysed the data set using the phylogenetic package PAUP 3.1.1 (Swofford, 1993) on a MacIntosh Quadra 700 computer. Because of the size of the data matrix, only the heuristic search option could be used.

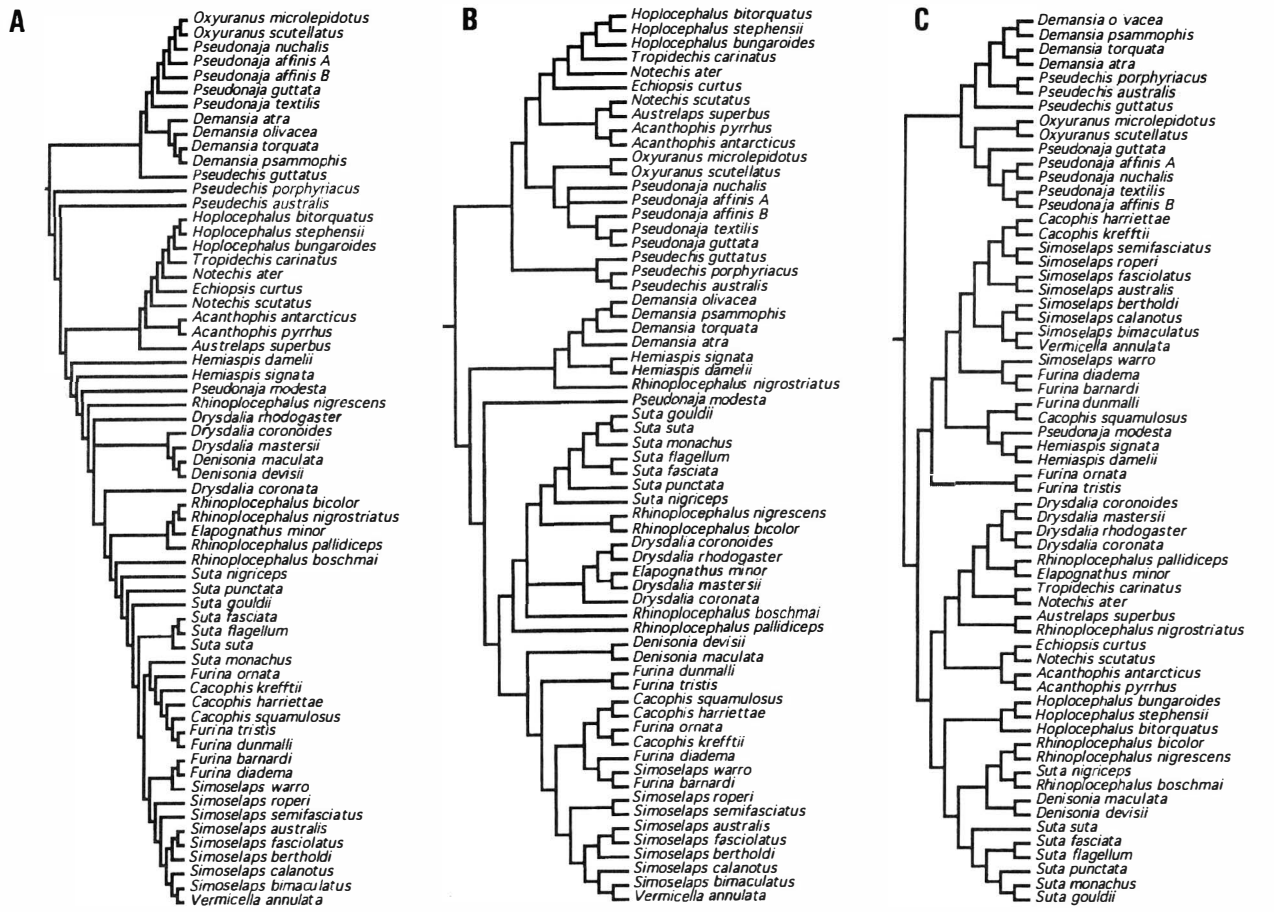

FIG. 1. The trees proposed for the data set in Table 1 (Wallach, 1985). A, tree found using the WAGNER algorithm of PHYSYS. Characters assumed to be reversible. B, tree found using the Pimentel algorithm of PHYSYS. Characters assumed to be reversible. C, tree found using the WISS algorithm of PHYSYS. Characters assumed to be irreversible.

Thus, as in the previous analysis, multistate characters were ordered, and each character state change (e.g. 0-1, or 2--1) was given a weighting of one. This has the undesirable effect that finely subdivided characters (those with more states) contribute more to tree length, and could have been eliminated by scaling all characters to unity. Also, some characters appear to be correlated (e.g. characters 19, tracheal rings with 21, tracheal lung). However, in order that my results be directly comparable to the previous study, no attempt has been made at this stage to modify the raw data set. In future, a more exhaustive study would need to increase sample sizes for many taxa, employ different outgroups, use organ mid-points rather than ends as landmarks, employ recent methods for coding continuous variables, consider character correlations, and investigate the effects of scaling all characters to unity (Wallach pers. comm., Underwood pers. comm.).

The analysis was run assuming that all characters were reversible (this corresponded to the Wagner and Pimentel analyses in PHYSYS). Two heuristic searches were performed: one using simple stepwise addition, and the other using 500 replicates of random stepwise addition. The latter is more time consuming but is usually better at finding all the most parsimonious trees.

A second analysis was run assuming irreversibility (this corresponded to the WISS analysis in PHYSYS). A heuristic search using simple stepwise addition was performed. Because PAUP is very slow when operating under this constraint, a search using random stepwise addition could not be performed (see Results).

RESULTS AND DISCUSSION

The re-analysis of Wallach's data set using PAUP 3.1.1, assuming reversibility, found a total of 258 equally-parsimonious trees, each of 578 steps. The search involving simple stepwise addition found only 27 trees, while the search involving random stepwise addition found 258 trees, including the 27 found in the former search. Thus, the analysis using random stepwise addition proved superior at finding the most parsimonious trees. All 258 trees were found in the first 200 random stepwise addition replicates, and the remaining 300 replicates only found trees already discovered in previous replicates. Thus, further replicates of random stepwise addition are unlikely to discover other equally-parsimonious (or even more parsimonious) trees, increasing one's confidence that all the most parsimonious trees were found.

The consistency index (0.147) and retention index (0.576) are both low, even when the number of taxa is

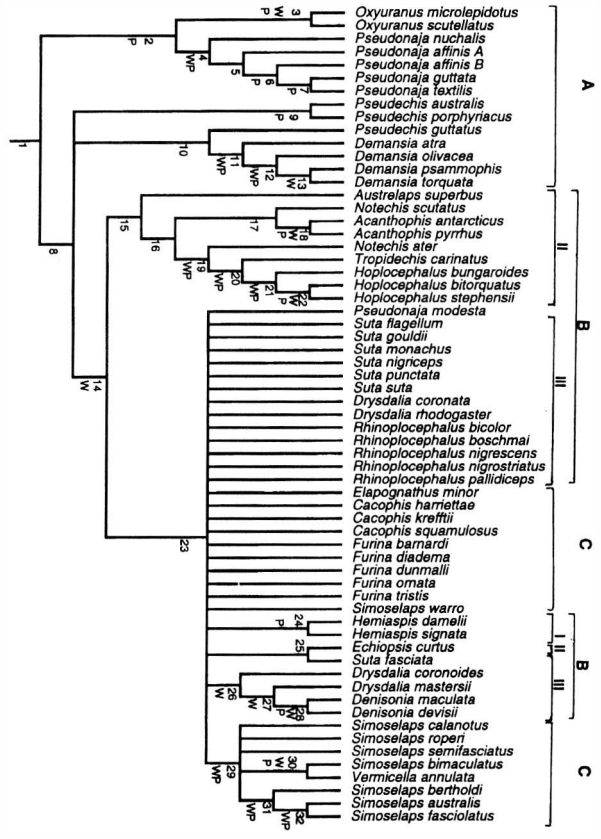

FIG. 2. Strict component consensus of the 258 most-parsimonious trees for the data set in Table 1, found using PAUP 3.1.1. The most parsimonious trees are each 578 steps long, c.i. 0.147, r.i. 0.576. Diagnoses for the numbered clades are presented in Table 2. "W" indicates a clade found in the corresponding Wagner tree (Fig. 1A), "P" indicates a clade found in the corresponding Pimentel tree (Fig. 1B). The taxa included in Wallach's divisions (A, BI, BII, BIII, C) are also indicated along the top of the cladogram.

taken into account (Sanderson & Donoghue, 1989), implying much character incongruence within the data set. The strict component consensus tree - which depicts only those clades common to all most-parsimonious trees (Wilkinson, 1994) - is shown in Figure 2A. Characters were optimized under delayed transformation, and characters diagnosing each grouping are listed in Table 2. It should be emphasized that, because of the amount of homoplasy in the data set, many characters can optimize in many different ways equally parsimoniously.

The Wagner tree (Fig. 1A) published in Wallach (1985) entails 592 steps. The Pimentel tree (Fig. 1B) is even less parsimonious, entailing 612 steps. Both trees are thus substantially longer than the most parsimonious trees (578 steps) found in this analysis. In addition, as noted by Wallach, they also differ very substantially from each other.

Both Wallach's trees are almost completely resolved, with only one or two trichotomies, while the consensus tree found in the current PAUP analysis is much more poorly resolved, with a 28-way polytomy. This polytomy mainly involves species in the genera

TABLE 2. Diagnoses of the clades identified in the PAUP analysis, when characters are optimized under delayed transformation. The numbered clades are shown in Fig. 2. Unless stated otherwise, changes are from 0-1. The consistency index for each character is also indicated in parentheses, characters with a relatively high index (0.33 or greater) are highlighted in bold. It will be clear that nearly all the characters are highly homoplastic.

1. 50 (0.22), 63 (0.083), 68 (0.111), 71 (0–2, 0.154).
2. 1 (0.111), 5 (0.125), 7 (0.167), 11 (0.048), 15 (0.067), 32 (0.1), 35 (0.067), 70 (0.2).
3. 38 (0.071), 39 (0.5), 51 (0.071), 59 (0–2, 0.286), 65 (0.2).
4. 46 (0.077), 49 (0.5), 57 (0.056), 61 (0.125).
5. 45 (0.095).
6. 17 (0.059).
7. 11 (1–0, 0.048), 23 (0.062), 38 (0.071).
8. 56 (0.095), 58 (0.074).
9. 9 (0.25), 57 (0.056), 60 (0.111), 64 (0.118), 72 (0.077).
10. 23 (0.062), 37 (0.091), 38 (0.071), 57 (0.056), 64 (0.118).
11. 11 (0.048), 41 (1.0), 56 (1–2, 0.095), 58 (1–0, 0.074), 61 (0.125), 64 (1–2, 0.118), 68 (1–2, 0.111), 70 (0.2).
12. 15 (0.067), 43 (0.2).
13. 17 (0.059), 18 (0.083), 33 (0.125).
14. 21 (0.056), 30 (0.5), 40 (0.167), 42 (0.2), 58 (1–2, 0.074). 72 (0.077).
15. 23 (0.062), 28 (0.1), 35 (0.067), 69 (0.2).
16. 56 (1–0, 0.095), 65 (0.2).
17. 15 (0.067), 21 (1–2, 0.056).
18. 23 (1–0, 0.062), 32 (0.1), 33 (0.125), 45 (0.095), 46 (0.077), 48 (0.333), 55 (0.5), 58 (2–1, 0.074), 68 (1–0. 0.111).
19. 10 (0.091), 11 (0.048), 13 (0.125), 19 (0.053), 21 (1–0. 0.056), 45 (0.095).
20. 5 (0.125), 66 (1.0), 69 (1–0, 0.2), 70 (0.2), 71 (2–1. 0.154).
21. 40 (1–0, 0.167), 44 (0.071), 49 (0–2, 0.5), 63 (1–0. 0.083), 68 (1–0, 0.111), 71 (1–0, 0.154).
22. 10 (1–0, 0.091), 13 (1–0, 0.125), 24 (0.059), 28 (1–0. 0.1), 42 (1–0, 0.2), 66 (1–2, 1.0).
23. 10 (0.091), 15 (0.067), 18 (0.083), 32 (0.1), 44 (0.071). 45 (0–2, 0.095), 56 (1–2, 0.095), 67 (0.286), 68 (1–0. 0.111), 71 (2–0, 0.154).
24. 23 (0.062), 31 (0.333), 32 (1–0, 0.1), 44 (1–0, 0.071), 45 (2–1, 0.095), 56 (2–1, 0.095), 57 (0.056), 61 (0.125), 64 (0–2, 0.118), 68 (0.111), 71 (0.154).
25. 1 (0.111), 5 (0.125), 7 (0.167), 16 (0–2, 0.062), 19 (0.053), 21 (1–2, 0.056), 45 (2–1, 0.095), 51 (0.071), 56 (2–1, 0.095), 68 (0.111), 69 (0.2).
26. 2 (0.143), 8 (0.067), 19 (0.053), 32 (1–0, 0.1), 68 (0.111).
27. 6 (0.083).
28. 56 (2–1, 0.095), 63 (1–0, 0.083), 65 (0.2), 69 (0.2).
29. 6 (0.083), 14 (0.053), 19 (0.053), 24 (0.059), 26 (0.067). 37 (0.091), 46 (0.077), 57 (0.056), 58 (2–0, 0.074), 60 (0.111), 62 (0.2), 63 (1–0, 0.083), 67 (1–2, 0.286), 72 (1–0, 0.077).
30. 1 (0.111), 5 (0.125), 6 (1–0, 0.083), 7 (0.167), 29 (0.2). 36 (0.5), 40 (1–0, 0.167), 50 (1–2, 0.222).
31. 16 (0–2, 0.062), 21 (1–0, 0.056), 23 (0.062), 60 (1–0. 0.111).
32. 4 (0.167), 6 (1–0, 0.083), 10 (1–0, 0.091), 56 (2–1. 0.095).

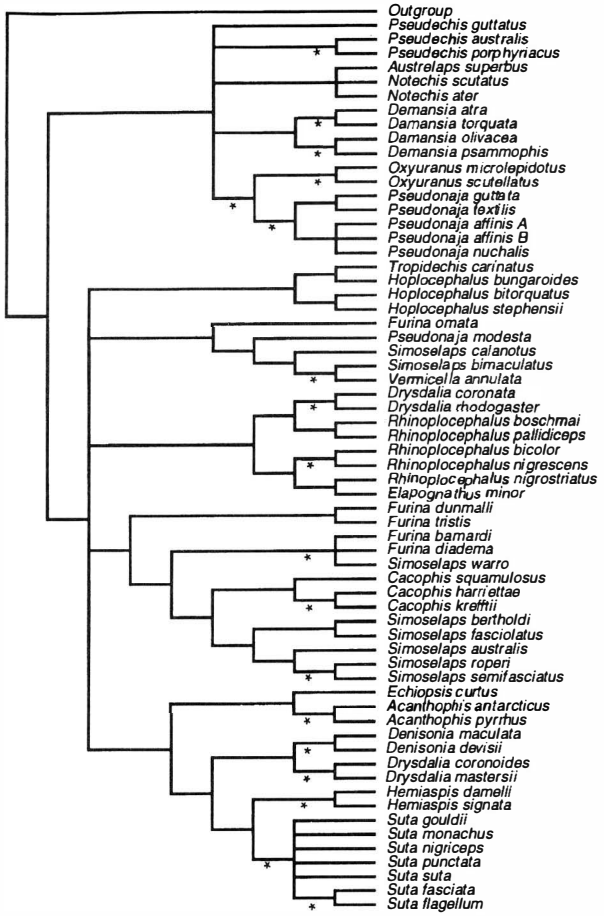

FIG. 3. The strict component consensus of the 840 trees, each 669 steps long, found in the PAUP analysis assuming irreversibility. The corresponding tree identified by the WISS algorithm in PHYSYS (Wallach, 1985) is very different (Fig. 1C): clades correctly identified in the WISS tree are indicated with an asterisk (*).

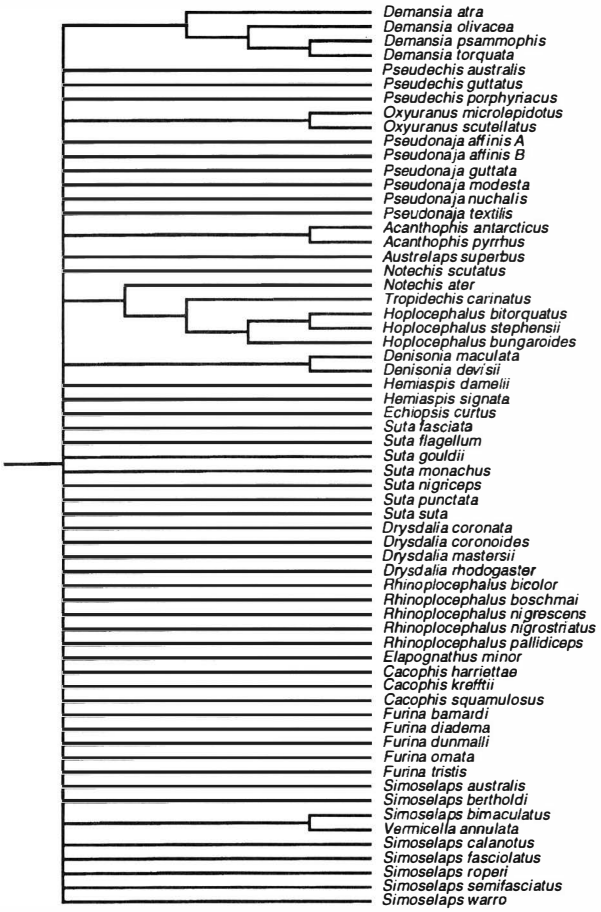

FIG. 4. The strict component consensus tree of the 32 700 cladograms of 578 or 579 steps in the heuristic search employing simple stepwise addition. The same tree was found in the search employing random stepwise addition. This tree is very poorly resolved.

Pseudonaja, Suta, Drysdalia, Rhinoplocephalus, Elapognathus, Cacophis, Furina, and *Simoselaps.* Another five-way polytomy involves mainly species of *Simoselaps*. When the trees are compared, of the 31 clades (clades 2-32 in Fig. 2A) identified in the PAUP analysis, only 13 were found in both the Wagner and Pimentel analyses. 3 were found in the Wagner analysis only, and 5 were found in the Pimentel analysis only. The correctly identified clades are shown in Figure 2A. It will be clear that the previous analyses were most accurate concerning relationships within the *Hoplocephalus-Austrelaps-Notechis* group and portions of the *Simoselaps-Vermicella* group. However, 10 of the clades in the PAUP consensus tree were not identified in either of Wallach's trees. In particular, many of the larger groupings found in the PAUP analysis (e.g. clades 8, 15, 23), representing the earliest and most basal divisions within Australian elapids, were not previously identified.

The PAUP analysis assuming irreversibility proved to be extremely slow. The heuristic search using simple stepwise addition took 242 hours (10 days) to complete. Extensive random stepwise addition would have taken much longer, and was therefore abandoned. The former analysis resulted in 840 equally-parsimonious trees, each of 669 steps. The strict component consensus tree is shown in Fig. 3. The corresponding WISS tree produced by PHYSYS (Fig. 1C) published in Wallach (1985) entailed 686 steps (when characters were optimized assuming irreversibility). Thus, the PHYSYS analysis again failed to find the most parsimonious solution for the data set, this time under the assumption of irreversibility. Again, of the 48 clades found in this analysis (not counting the clade consisting of the entire ingroup), only 18 were correctly identified. These are indicated in Fig. 3.

The above results demonstrate that the computer package available at the time did not allow Wallach to find the most parsimonious trees consistent with his data matrix in any of his three analyses. This is understandable, considering the size of the data set and the primitive nature of computer parsimony programs at the time. The consensus tree in each analysis is of a different topology, and less well resolved, than those published in Wallach.

Based primarily on the three trees found in his PHYSYS analyses, Wallach proposed some suprageneric groupings of Australian elapids. The assumption of irreversibility in cladistic analyses cannot usually be justified, and I know of no recent cladistic

analyses of snake phylogeny that make this assumption. For this reason, in the following discussion, I will only compare in detail Wallach's proposed divisions with the PAUP consensus tree found for that data set assuming reversibility.

The major clades ("Divisions", divided into "Sections") proposed by Wallach are indicated in Fig. 2A, and discussed below.

Division A: *Pseudechis, Demansia, Pseudonaja* (excluding *P. modesta*) and *Oxyuranus*. This assemblage is paraphyletic in this analysis. While these taxa are similar, it appears that the similarities they share are all primitive for Australian elapids. As noted by Wallach, *Pseudonaja modesta* surprisingly comes out as being not closely related to other members of the genus. Rather, it is much more derived than any of the members of Division A, and has affinities with Division C.

Division B: Hemiaspis, Hoplocephalus, Tropidechis, Notechis, Austrelaps, Echiopsis, Acanthophis, Rhinoplocephalus (including *Cryptophis*), *Suta* (*"Parasuta"*), *Drysdalia* and *Denisonia*. This grouping includes all the viviparous forms, with the exception of *Pseudechis porphyriacus*. As noted by Wallach, *Pseudonaja modesta* surprisingly comes out as part of this group, rather than being related to other species of *Pseudonaja*. The most parsimonious arrangement found in this study indicates that this group is paraphyletic with respect to Division C: *Simoselaps, Furina, Vermicella,* and *Cacophis*.

Division B, Section I: Hemiaspis. The monophyly, and distinctness, of this genus is supported here. It is not closely related to any other genus in Division B.

Division B, Section II: Hoplocephalus, Tropidechis, Notechis, Austrelaps, Echiopsis, Acanthophis. This grouping is largely supported by this analysis. All the genera, except for *Echiopsis,* form a clade. *Echiopsis* is not part of this lineage, but clusters with *Suta fasciata*.

Division B, Section III. Rhinoplocephalus (including *Cryptophis*), *Suta* (*"Parasuta"*), *Drysdalia* and *Denisonia*. Whether this grouping is monophyletic or paraphyletic cannot be ascertained; i.e. this is a "metataxon" (Archibald, 1994). This assemblage forms part of the 28-way polychotomy along with members of Division C.

Division C. Simoselaps, Vermicella, Furina (including *Glyphodon*), *Cacophis*. Monophyly or paraphyly of this group cannot be ascertained, this grouping is therefore another "metataxon" (Archibald 1994). Again, the contained taxa form part of the 28-way polychotomy along with members of Division B.

The soft anatomical data set therefore does not resolve the phylogenetic relationships of Australian elapids as fully as previously thought. Wallach (1985) was careful to emphasize that his results were tentative, because of the inadequate sample sizes of many taxa: most species were represented by only one or two specimens. Another source of error could not be detected at the time: the failure of the computer programs to find the most parsimonious tree. Most of the groupings found in Wallach's analyses, and proposed in his dicussion, are not found in the PAUP analysis. However, many of Wallach's groupings, including those above, have been accepted by later workers. For instance, Hutchinson (1990), in his taxonomic revision of generic names, cited Wallach's work as containing evidence for the monophyly of *Drysdalia*, the monophyly of *Furina*, the monophyly of *Pseudechis,* and a close relationship between *Echiopsis* and *Notechis*. The present study shows that Wallach's data set does not support any of these conclusions. However, Wallach's analyses managed to identify many of the clades present on the most parsimonious trees (Figure 2A).

Because the consistency index for this analysis was rather low (0.147), implying much character incongruence, it was decided to investigate the strength of the phylogenetic signal in the data. I first attempted to calculate the Bremer index for each clade. This index is the number of steps it takes to break up a clade (Bremer 1988). The procedure is discussed in Lee (1995, 1996). Briefly, in order to obtain the Bremer index of, for instance, the *Oxyuranus* clade, a constraint tree is entered into PAUP. In this tree, the two species of *Oxyuranus* form a clade, but relationships between the *Oxyuranus* clade and all other ingroup taxa, are unresolved. PAUP is then instructed to find the most parsimonius tree which is *not* consistent with this constraint tree (reverse searching). The difference between the length of this tree (584) and the most parsimonious tree (578 steps) is the Bremer index. It soon became apparent that the data set was too big for PAUP to find the most parsimonious tree during reverse searching, and thus Bremer indices could not be calculated. For instance, according to several different heuristic analyses in PAUP, the most parsimonious trees inconsistent with the *Oxyuranus* clade are each 584 steps, in which case the Bremer index is 6. However, this clade (Table 2) is only diagnosed by five characters, and hence can be broken by assuming, at most, 5 additional steps. Since all the characters are equivocal, one would expect to be able to break up the clade by assuming fewer than 5 additional steps. Thus, the most parsimonious tree inconsistent with *Oxyuranus* monophyly should have been 583 or fewer steps, and could not be the 584 calculated by PAUP's reverse search. For this reason, Bremer indices were not calculated via this method. However, it was possible to use another method to identify clades with a Bremer index of only 1 (see below).

Because of the number of taxa, it also did not prove possible to investigate the strength of the clades via bootstrapping (Felsenstein, 1985; Sanderson, 1995): an attempt was made, but was aborted after 24 hours elapsed and only three replicates (out of the minimum 100 needed) were completed.

One further test, however, could be performed to test the strength of the phylogenetic signal in the data set. The PAUP analysis (assuming reversibility) was rerun, and all most parsimonious trees, and those one step longer, were saved. Using simple stepwise addition, a

total of 32 700 trees (27 of 578 steps, the remainder of 579 steps), were identified before the computer ran out of memory, and the strict consensus tree of all these trees is almost totally unresolved (Fig. 4). An analysis employing random stepwise addition was also performed; in order to stop the computer memory from being filled with trees from a single replicate, PAUP was instructed to save no more than 1000 trees from each replicate. The strict consensus from this analysis was identical to the one found in the preceding analysis. Thus, almost all the clades identified in the analysis can be collapsed if one assumes only a single additional step, i.e., most clades have a Bremer index of only 1.

The above analyses demonstrate that this soft anatomical (visceral and external morphological) data set is much less phylogenetically informative than previously thought. They also show how the number of changes diagnosing a clade is often a poor indicator of the strength of the grouping: most of the groupings in this analysis collapse if one assumes a single additional step (Fig. 4), yet many of these are diagnosed by numerous changes (Table 2).

The weak and ambiguous phylogenetic signal in this data set means that one should avoid making evolutionary inferences or taxonomic changes based on the most parsimonious trees, or Wallach's published trees. It should be mentioned, though, that recent taxonomic reviews (Hutchinson, 1990) and ecological studies (Shine, 1994) of Australian elapids have not been based solely on Wallach's data, but have also considered other phylogenetic evidence (e.g. Mengden, 1985; Schwaner *et al.*, 1985).

Nevertheless, Wallach's data set remains an extremely important body of work: in particular, it is one of the most comprehensive surveys of morphology and variability of the viscera in any group of snakes. The fact that it is not very phylogenetically informative is in itself a significant and potentially profound conclusion. It may be that the data were inadequately coded, and that a rigorous re-study might reveal a stronger phylogenetic signal. Alternatively, one might conclude that visceral and scale features, the bulk of the data set, are too labile to be very useful in constructing higher level (suprageneric) groupings, i.e. the poor signal is real rather than an artefact. However, many other studies of snakes have suggested the potential value of visceral and scale character data in higher-level squamate phylogeny, e.g. Underwood (1967), Rossman *et al.* (1982), Becker *et al.* (1989), Underwood & Stimson (1990). Much more work is necessary in order to test this hypothesis. For instance, a best fitting tree will need to be found from a combined analysis of osteological, myological, visceral, external, genetic, behavioural, and ecological traits, and relative amounts of homoplasy in each data set compared.

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STAGE-FREQUENCY AND HABITAT SELECTION OF A COHORT OF *PSEUDACRIS OCULARIS* TADPOLES (HYLIDAE: ANURA) IN A FLORIDA TEMPORARY POND

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An analysis of major demographic characteristics of a cohort of *Pseudacris ocularis* tadpoles was performed under natural conditions. The study was carried out in a temporary pond within the Lower Suwannee National Wildlife Refuge, in Florida, USA. Five developmental stage-groups were established. Several samples were taken at different times during development of the cohort. The pond water-level was nearly constant throughout the study. The main results obtained were: (1) the mean time to metamorphosis was 7.31 d; (2) the tadpoles spent more time at stages 33-36 (2.42 d) than at other stages; (3) the shortest developmental stages were 25-28 (only 0.99 d); (4) the survival rate was 10.3%; (5) the range of the survival rate for the five stage-groups was 47.1-73.6%; (6) the estimated unit time survival rate was 73.3%; (7) the life expectancy (e(x)) for a tadpole just hatched was 3.07 d; (8) the survival curve (l(x)) was comparable to a Type II curve; and (9) the value of H (entropy) was 0.824. The tadpoles spent more time at the periphery than in the centre of the pond. Significant differences in water temperatures between the peripheral and central sampling units were observed.

INTRODUCTION

Organisms in seasonal and temporary habitats should time their reproduction to synchronize with predictable changes in environmental quality that optimize offspring survival and growth. Nevertheless, populations frequently have more than one time for reproduction during each annual cycle. A temporary pool habitat has two important characteristics for tadpoles, which begin to develop soon after the pond fills with water. First, explosive primary productivity stimulates rapid growth (Wassersug, 1975). Second, fish and other large predators are absent. Some predators (e.g. many predaceous insects) do not colonize such ponds until some time after the ponds have been filled, and tadpoles may be able to grow fast enough to be too large to be eaten before encountering such predators (Grubb, 1972; Wilbur, 1980). However, these advantageous characteristics can be countered by mortality caused by predaceous insects that colonize temporary ponds at the same time that the amphibians deposit their eggs (Brockelman, 1969; Heyer *et al.*, 1975; Caldwell *et al.*, 1980; Smith, 1983; Crump, 1984; Kehr & Schnack, 1991). Nevertheless, the biotic factors can be minimized by the influence of abiotic effects (Warner *et al.*, 1991). Pond desiccation is one of the most important factors acting as a regulator of larval amphibian populations (Heyer, 1973; Seale, 1982; Semlitsch, 1987).

Stage-frequency models are based on counting or estimating the number of individuals in different developmental stages and at several times while a population is developing. Stage-frequency data in nature are important for several reasons. First, they allow the dynamics of the population to be analyzed. Second, stage-frequency data can be used to estimate and compare population parameters among populations of the same or different species. Third, depending on the model used, it is possible to use stage-frequency data to simulate population dynamics. These simulations are useful when one is concerned about whether populations are increasing or declining. There are many methodologies for analysing stage-frequency data. Sophisticated and relatively simple mathematical models have been developed, many of them recently reviewed by Manly (1989, 1990). These models have been developed largely for analysing insect populations. Nevertheless, they have also been used successfully in tadpole studies (Kehr & Adema, 1990; Kehr & Basso, 1992).

In this study, the stage-frequency of a cohort of *Pseudacris ocularis* tadpoles developing in a temporary pond was analysed. The objectives were to determine: (1) the number of tadpoles entering each stage; (2) the time duration (in days) of each stage; (3) the stage-specific survival rate; and (4) the survival rate per unit time. With the stage-frequency data obtained from the field, a horizontal life table was developed. The purpose of this table was to examine other demographic characteristics of the cohort. The demographic statistics that this table reveals, among others, include: (1) survival rate (l(x)) of the cohort to different developmental stages, (2) expectation of life (e(x)) of the tadpoles; and (3) the frequency distribution of deaths in the cohort (d(x)). The spatial distribution of tadpoles was also examined in order to establish temporal differences in dispersion related to developmental stages. To my knowledge, there have been no previous reports on the population ecology of this species under natural conditions.

TABLE 1. Stage-frequency data recorded for a population of *Pseudacris ocularis* tadpoles. The Roman numerals represent five groups of stages defined for this study. Numbers in parentheses are the developmental stages (Gosner, 1960).

Date	Day	I (25-28)	II (29-32)	III (33-36)	IV (37-40)	V (41-43)	TOTAL
3/10/92	0	0	0	0	0	0	0
3/14/92	4	5	1	0	0	0	6
3/18/92	8	6	5	0	0	0	11
3/25/92	15	12	20	4	0	0	36
4/02/92	23	3	5	11	4	6	29
4/09/92	30	0	0	2	3	1	6
TOTAL		26	31	17	7	7	88

MATERIALS AND METHODS

Pseudacris ocularis (Hylidae) is the smallest North American frog, and reaches no more than 18 mm SVL. The range of this species extends from south-eastern Virginia to the southern tip of Florida, and inland to the edge of the Piedmont and to the extreme south-east of Alabama (USA) (Conant & Collins, 1991). This species generally breeds in flooded grassy areas, although it also can be found in permanent ponds. Most breeding activity occurs in March and April, and can begin as early as January in Florida. *Pseudacris ocularis* lays its eggs in a mass of approximately 100 eggs (Ashton & Ashton, 1988).

The study site was a temporary pond in the Lower Suwannee National Wildlife Refuge (28°30' N, 83°15' W), situated along the southern edge of the Big Bend region of Florida's west coast in Dixie and Levy counties. Cypress and hardwood forests surrounded the circular pond which was 9±1.5 m in diameter and had maximum and minimum depths of 30 and 10 cm. The pond formed with heavy rains on 10 March, and the surface was in full sunlight by midday when samples were taken.

The pond was sampled once per week (Table 1) from March - April 1992, starting on March 14th, four days after heavy rain. These initial tadpoles were at stages 25-29 (Gosner, 1960). All tadpoles were considered the same cohort. The pond was divided into eight wedge-shaped sections, and two samples (30 cm and 150 cm from shore) were taken from each section at each visit (n= 16). The sampling points were constant throughout the study. Each sample was taken with a rectangular-framed dip net with fine mesh (width 1 m; height 0.45 m; and depth 0.45 m). The dip net was dragged for 1 m along the bottom at each sampling point and always from the outside towards the centre of the pond.

Tadpoles were transported to the laboratory where developmental stages (Gosner, 1960) were recorded. The developmental stages were divided into five groups: I: stages 25-28; II: 29-32; III: 33-36; IV: 37-40, and V: 41-43. Metamorphic individuals were those having 4 legs exposed (> stage 43). All tadpoles were returned to the pond within 24-48 hr of collection and released at the sampling point at which they had been captured. No animals died during transit or laboratory examination. Water temperature at 5 cm depth was recorded on each sampling day at the centre and periphery of the pond. One water sample per day was randomly taken and analysed for pH.

STAGE-FREQUENCY MODELS

Three different methods were applied to the data, but only the results from the method that provided the best fit are discussed in the Results section. The methods were selected for the simplicity of the parameter estimations, the matrix of data obtained, and the two factors cited in the previous paragraph. Though the parameters obtained from these models are similar, the methods for obtaining them are different. The first method used was the K-N-M model developed by Manly (1985). This model is an extension of the Kiritani & Nakasuji's method (1967) made more useful by Manly. Its principal strength is its flexibility in relation to the beginning of sampling. Furthermore, sampling need not continue until all individuals are dead. This model assumes a constant survival rate per unit time for all stages.

A second method tested was the multiple regression method also developed by Manly (1987). This model permits different stages to have different survival rates per unit time, with survival constant with the time. The third method applied was the Kempton model (1979). This model is also flexible because it permits different distributions of the entry times into stage 1 (e.g., gamma, normal and inverse normal distributions), which are similar to the distributions of the stage-durations. The model assumption is that the survival rate per unit time is the same for all stages, but is variable with time.

HORIZONTAL LIFE TABLE CONSTRUCTION

A horizontal life table (Carey, 1993) was constructed from the number of tadpoles entering each

group obtained from the stage-frequency model, and the number of tadpoles surviving at each day was calculated. Entropy (H) was first used by Demetrius (1978, 1979). This value represents the quantitative survival pattern of a cohort studied and allows comparison among cohorts or populations of the same or different species. If H= 0, all animals die at the same age, and if H=1, then l(x) decreases exponentially.

RESULTS

FREQUENCY STAGES

The model that best fit the field data (Table 1) was the K-N-M model (Manly, 1985, 1989, 1990). The Kempton model (1979) also fit the data (considering a normal distribution of the entry time to stage-group I), after the transformation of each data point (due to extraneous variation) through a heterogeneity factor (Manly, 1990). But even after that transformation, the K-N-M model provided a better fit.

Table 2A summarizes the results obtained by the K-N-M model. The estimated unit time survival rate was 0.733. The survival rate in the cohort studied was 10.3%. Tadpoles in group I had the highest survival rate and spent only 1 day at this stage. In contrast, tadpoles in group III had the lowest survival rate and stayed an average of 2.42 days at that stage. Stage specific survival rate, considering all groups, ranged from 47.1 - 73.6%. The mean total time for a tadpole in group I (stages 25-28) to reach group V (stages 41-43) was 7.31 days. Tadpoles from group V spent less than 24 hr in that group in the laboratory.

The accuracy of the model was analysed through the simulation of 1000 data sets (Manly, personal communication) by simulation method 2 (Manly, 1990). This method is based on using a specific stage-frequency model (K-N-M model in this study) for calculating expected population stage-frequencies, and it is possible to calculate stage-frequencies by generating independent Poisson variates with those expected values. The estimates of the expected frequencies are calculated as functions of the entry distribution to group I and considering the distribution of stage durations. The error (standard deviation, SD) of each simulated data set was analyzed in comparison with the error SD obtained from the model fitted to the observed data (Table 2B). Because, 80.2% of the simulated data sets had an error SD $\leq$ 4.5, the K-N-M model provides a good fit to the observed data set.

TABLE 2. Results obtained from the application of the stage-frequency K-N-M model (Manly, 1985) to a cohort of *Pseudacris ocularis* tadpoles. (A): groups I - V (defined in Table 1). (B): Expected sample frequencies obtained from the application of K-N-M model. Error SD= sum of squares of differences between observed (Table 1) and expected stage-frequencies. 1000 data sets were simulated through expected sample frequencies; 802 data sets gave an error SD $\leq$4.5, suggesting a good fit for the data to the K-N-M model.

(A)

Group	Survival rate	Duration (days)	Tadpoles Entering
I	0.736	0.99	184.6
II	0.517	2.12	135.9
III	0.471	2.42	70.3
IV	0.574	1.78	33.1
V	/	/	19.0

THETA= 0.3105

Estimated unit time survival rate (0)= e^{-THETA} = 0.733

(B)

	Group					
Days	I	II	III	IV	V	TOTAL
0	0	0	0	0	0	0
4	6	2	0	0	0	8
8	18	3	1	0	0	22
15	22	8	4	1	0	35
23	15	7	5	2	2	31
30	1	1	2	2	2	8
TOTAL	62	21	12	5	4	105

Error SD= 4.5

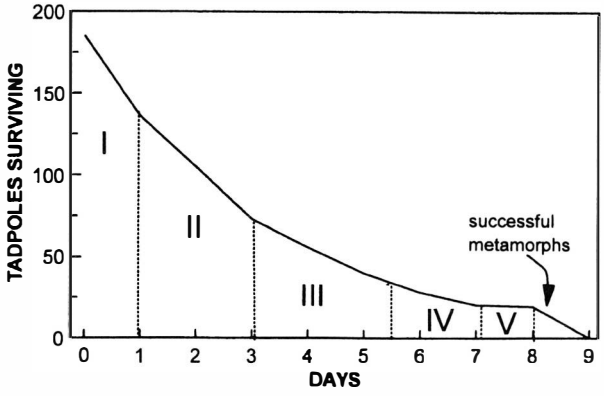

FIG. 1. Number of *Pseudacris ocularis* tadpoles entering each group of stages (Table 2A). The broken line represents the duration (accumulated days) in each stage group. The number of tadpoles was rounded to the nearest integer. From this figure it was possible to obtain the number of tadpoles surviving each day and then to construct the horizontal life table (Table 3). The duration of the tadpoles in group V was just one day. Mortality in group V was zero. Nineteen tadpoles metamorphosed.

TABLE 3. Statistics estimated from the horizontal life table (according to the methodology proposed by Carey, 1993). The data were obtained from the interpolation for each day of the results shown in Fig. 1. Age(x)= age in days; Number of tadpoles= number observed each day; l(x)= fraction living at age x; p(x)= fraction surviving from x to x+1; q(x)= fraction dying from x to x+1; d(x)= fraction dying in interval x to x+1; L(x)= days lived in interval; T(x)= days lived beyond age x, and e(x)= expectation of life. H (entropy)= value that represents quantitatively the cohort survival pattern (on a scale from 0 - 1, for further explanation see text). ω= maximum age. Nineteen tadpoles reached metamorphosis.

Age (x)	Number of tadpoles	l(x)	p(x)	q(x)	d(x)	L(x)	T(x)	e(x)
0	185	1.000	0.735	0.265	0.265	0.868	3.078	3.078
1	136	0.735	0.772	0.228	0.168	0.651	2.211	3.007
2	105	0.568	0.695	0.305	0.173	0.481	1.559	2.748
3	73	0.395	0.767	0.233	0.092	0.349	1.078	2.733
4	56	0.303	0.714	0.286	0.086	0.259	0.730	2.411
5	40	0.216	0.700	0.300	0.065	0.184	0.470	2.175
6	28	0.151	0.714	0.286	0.043	0.130	0.286	1.893
7	20	0.108	0.950	0.050	0.005	0.105	0.157	1.450
8	19	0.103	0.000	1.000	0.103	0.051	0.051	0.500
9	0	/	/	/	/	/	/	/

H (entropy)= $\{\sum_{x=0}^{\omega} e(x)d(x)\}/e(0)$= 0.824

HORIZONTAL LIFE TABLE

The results obtained are summarized in Table 3. A linear regression was run using the logarithm of the number of tadpoles surviving as the dependent variable and the days of development as the independent variable. The results ($\log_{10} y = 2.422 - 0.190\ x$; r = -0.89, n = 10; $F_{1,8}$ = 30.67, P< 0.001) explain the good fit of l(x) to a linear model. The survivorship curve (l(x)) observed in this cohort is similar to a Type II curve proposed by Deevey (1947) (Fig. 2a). Furthermore, the trend in l(x) can be validated by the constant mortality rates (q(x)) observed primarily in the first six days (about 75% of life cycle) (Fig. 2b).

A newly hatched tadpole has a life expectancy of 3.07 days (Fig. 2a; Table 3). The declination of the life expectancy curve is practically constant with each day lived. This tendency indicates the lack of a strong mortality period. Although the greatest mortality frequency (d(x)) was observed in the first three days of development (Fig. 2b; Table 3), it was not significantly greater than in any other interval. The value of H obtained in this study was 0.824. It represents the percentage of change in life expectation owing to a 1% reduction in mortality at all ages (Table 3).

HABITAT SELECTION

The number of tadpoles collected in the central versus the peripheral samples was compared through the Interaction or Heterogeneity G-test (Sokal & Rohlf, 1981). This test partitions results into (1) a "heterogeneity" G to test whether habitat selection of the tadpoles was similar within each sample taken, and (2) a "pooled" G to test the tadpole preference (between cen-

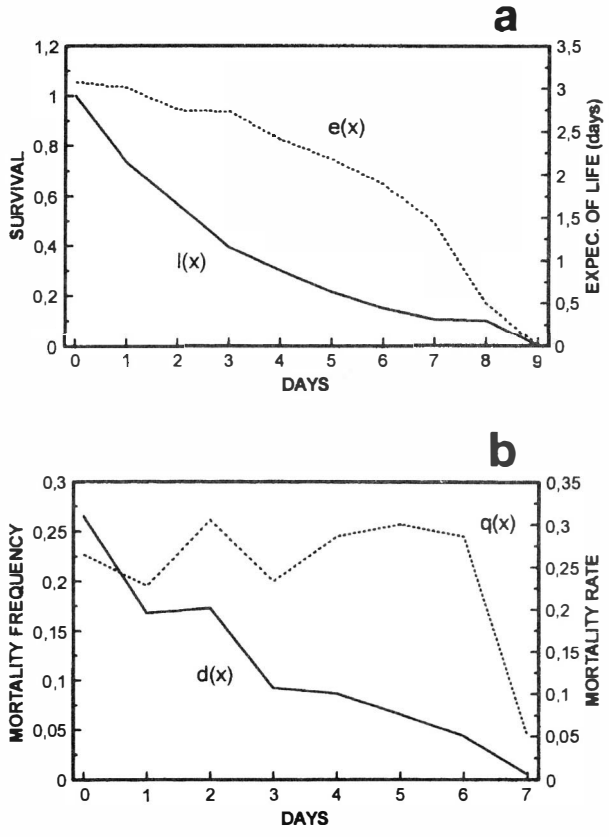

FIG. 2. Demographic estimations of the cohort of *Pseudacris ocularis* tadpoles (Table 3). a: survival rate (l(x)) and expectation of life (e(x)) in relation to developmental time. b: frequency of deaths (d(x)) and mortality rate (q(x)) in relation to developmental time.

TABLE 4. Calculation of the Heterogeneity *G*-test of the differences between the *Pseudacris ocularis* tadpoles located in the central and peripheral sampling units for each sample. *Significant ($P < 0.05$).

Samples	Sampling units location: central	peripheral	*n*		df	*G*
1	3	3	6		1	0.00
2	4	7	11		1	0.83
3	8	28	36		1	11.77*
4	15	14	29		1	0.03
5	1	5	6		1	2.91
				Total	5	15.54*
	31	57	88	Pooled	1	7.79*
				Heterogeneity	4	7.75

tral vs. peripheral samples) during the whole study. The "heterogeneity" *G* show no tendency for the tadpoles to select either habitat in four samples ($P > 0.05$, Table 4). In the remaining sample (sample 3), which had the largest sample size (36), the tadpoles showed a significant tendency to select the periphery of the pond ($P < 0.05$, Table 4). When tadpole density was higher (3rd sample) the developmental stages were low and these tadpoles selected the periphery rather than the centre of the pond. The "pooled" *G* test result shows that of 88 tadpoles collected in this study, the tadpoles significantly selected the peripheral habitat (57 tadpoles vs. 31 tadpoles) ($P < 0.05$, Table 4).

Water temperature in the peripheral and central sampling units differed significantly (Wilcoxon paired-sample, $T+ = 15$, $n=5$, $P = 0.03$). The peripheral water temperature was consistently higher than the central water temperature (Table 5). The range of the pH measured in all samples was 6.55-6.72.

Significant differences were not observed between the developmental stages of tadpoles found in the central and peripheral sampling units within each sample (Mann-Whitney *U* test, (two tailed test): [first sample: $U = 7.24$, $n_1 = 3$ $n_2 = 3$, $P = 0.5$; second sample: $U = 17.1$, $n_1 = 4$ $n_2 = 7$; $P = 0.84$; third sample: $U = 130$, $n_1 = 8$ $n_2 = 28$, $P = 0.5$; fourth sample: $U = 118.5$, $n_1 = 15$ $n_2 = 14$, $P = 0.56$]). Only the tadpoles of the first four samples were considered for this test (Table 5). Furthermore, no significant differences were found among the developmental stages of the eight peripheral sampling units nor among the eight central sampling units within each sample day (Kruskal-Wallis test [first sample - periphery: $H = 2$, $P = 0.36$; centre: $H = 0$, $P = 1$; second sample - periphery: $H = 2.7$, $P = 0.26$; centre: $H = 0.65$, $P = 0.72$; third sample - periphery: $H = 12$, $P = 0.06$; centre: $H = 5.35$, $P = 0.25$; fourth sample - periphery: $H = 4.96$; $P = 0.29$; centre: $H = 3.93$, $P = 0.68$; fifth sample - periphery: $H = 3.8$, $P = 0.28$; centre: only one tadpole]). Nevertheless, the peripheral sampling point data on the third sample day could be considered "suggestive". They suggest a weak trend toward a heterogeneous distribution in the periphery of the pond.

DISCUSSION

The population model of best fit to the cohort of *Pseudacris ocularis* tadpoles was the K-N-M model, which supposes a constant survival rate per unit time for all stages. The Kempton model, which also provided a good fit to the observed data, but not as good as K-N-M, similarly assumes that survival rate per unit time is the same for all stages although variable with time. Although this is somewhat simplistic, a causal factor for this mortality pattern may be the small body size of the *P. ocularis* tadpoles which leaves them almost continuously vulnerable to predators.

The survival rate per each group depended directly on the time spent by the tadpoles in each group, the longer time in each group, and the higher mortality independent of the body size of the tadpoles. Mortality agents acting on these tadpoles are not density-dependent. Food supply and the relatively lower tadpole

TABLE 5. Developmental stages of *Pseudacris ocularis* tadpoles according to the sampling location. Water temperatures are °C.

Samples:		25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	≥41	Total	Water temp.
1	Central	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	3	15.8
	Peripheral	-	1	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	3	16.0
2	Central	1	1	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	4	20.7
	Peripheral	1	1	1	1	2	1	-	-	-	-	-	-	-	-	-	-	-	7	21.0
3	Central	-	-	-	1	3	1	2	-	1	-	-	-	-	-	-	-	-	8	23.1
	Peripheral	5	3	1	2	4	3	2	5	3	-	-	-	-	-	-	-	-	28	23.4
4	Central	-	-	-	1	-	-	-	3	-	3	-	1	2	1	1	-	3	15	18.2
	Peripheral	-	1	1	-	-	-	1	1	1	1	2	3	-	-	-	-	3	14	18.4
5	Central	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	26.1
	Peripheral	-	-	-	-	-	-	-	-	-	-	1	1	1	-	1	-	1	5	26.3

densities were factors clearly not related to tadpole mortality. The survival rate of 10.3% is high compared with what has been reported for other species (Herreid & Kinney, 1966; Brockelman, 1969; Calef, 1973; Kehr & Basso, 1992). Frequently, the survival rate to metamorphosis is less than 5% (Crump, 1984). In most tadpole population studies, poor survival rate has been associated principally with high predation. Nonetheless, the high survival rate of *P. ocularis* in this study has been observed in spite of the influence of natural predators. The potential predators observed were the nymphs of Odonata (*Pachydiplax longipennis*). The relationship between insect predators and tadpoles is body size dependent (Wilbur, 1980; Crump, 1984). This predator-prey relationship must be strongly influenced when the tadpoles have large changes in body size during their development. The maximum body size in *P. ocularis* tadpoles is small and possibly always within the body ranges for naiad predation.

The cohort survival curve is comparable to a Type II survivorship curve (Deevey, 1947), suggesting a similar survival rate for each age class with the number of tadpoles in the cohort declining exponentially. On an arithmetic scale, the survival rate is concave. These results corroborate the opinion of Petranka (1985), who in re-evaluating data from other tadpole studies, concluded that the Type II curve is very common in tadpoles and that in many cases data were misinterpreted as Type III curves. The life expectancy curve (e(x)) of the *P. ocularis* tadpoles declined steadily with time without any ascending peaks that would show a strong mortality period. The life expectency for a *P. ocularis* tadpole that just hatched is 3.08 days, or about 42% of the average time from hatching to metamorphosis.

There are many interpretations about entropy (H) in population dynamics. The entropy observed in this cohort (0.82) might also be interpreted as: (1) the proportional increase in life expectancy in a tadpole just hatched if each first death were prevented, or (2) the number of days missing because of death per number of days lived (Carey, 1993). I know of no other entropy values for tadpole populations for comparison. It is probable that the entropy value for *P. ocularis* tadpoles is low compared to other species.

The time to metamorphosis in *P. ocularis* tadpoles is very short. Ashton & Ashton (1988) reported the time to metamorphosis as approximately 10 days, but did not indicate whether the tadpoles were raised under laboratory or natural conditions. The mean developmental time for the tadpoles in my study under natural conditions was 7.31 days. A short time to metamorphosis is crucial to *P. ocularis* tadpoles considering the ephemeral characteristics of the habitat in which they live, where desiccation is common. Although synergistic abiotic and biotic factors can influence tadpole development, the effect of a drying environment has probably been the major selective force for rapid development in this species.

Although it was not observed in all stages, the tadpoles of *P. ocularis* below stage 33 spent more time in shallow water than in deep water, when these stages had the greatest densities in this cohort. The temperature in the periphery was higher than in the centre of the pond, and presumably temperature variation in the periphery was greater. This behaviour might be related to habitat selection for preferred temperature by the youngest tadpoles. According to Dupré & Petranka (1985), physical factors generally covary making it difficult to establish which factors significantly influence tadpole development. However, the role of temperature on tadpole habitat selection has been examined in some studies (Brattstrom, 1962; De Vlaming & Bury, 1970; Hutchison & Hill, 1978). Most of the studies have reported a thermal preference in tadpoles that increases with the developmental stage, until they reach metamorphic climax. The behaviour observed in *P. ocularis* tadpoles contrasts with that reported previously. Although this behaviour, in principle, might enhance growth rate, differences in developmental stages were not significant between the periphery versus central samples. Also, differences in developmental stages were not observed among those tadpoles localized in the peripheral samples. There are other arguments for explaining this spatial behaviour. Predators (Petranka, 1983), light (Beiswenger, 1977), food distribution, among others, can strongly influence the spatial distribution of tadpoles. Therefore, it would be necessary to conduct more specific experiments in natural conditions to establish the basis for tadpole differential habitat selection.

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SHORT NOTES

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A CONSIDERATION OF THE PHYLOGENETIC SIGNIFICANCE OF ACRODONTY

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It is widely held that the acrodont tooth implantation is the derived condition within Squamata. However, Witten (1994) has recently questioned the polarity of this character and he claims that acrodonty is primitive for Squamata. The definition of apical attachment is usually given to the term acrodont (Edmund, 1969). However, very few squamates bear truly apical teeth. The acrodont teeth of agamids and chamaeleontids are always both apical and mesial, not solely apical, although they may be attached closer to the apex than many pleurodont teeth. Thus, the traditional definition of acrodont teeth is rather misleading in squamates and needs a reappraisal. Robinson (1976) used another definition and she indicates that acrodont teeth are fused with the bone of attachment. Such a definition is equally applicable to a pleurodont dentition, because pleurodont teeth are also fused to the lingual surface of the jaw. Alifanov (1989) coined the term "subacrodont" to designate an intermediate condition between acrodonty and pleurodonty. Moreover, tooth attachment in varanids is on an obliquely sloping bony surface (subpleurodont teeth, after Hoffstetter, 1954). However, if the acrodont type of insertion is not clearly defined, it seems that there is an acrodont mode of tooth replacement, or more exactly, absence of replacement. Worn teeth are not replaced and new teeth appear at the rear of the tooth row. Acrodont teeth of squamates may also be characterized by morphological characters, such as the presence of lateral occlusal wear and acrodont dentition is generally associated with the lack of a true dental shelf which supports the tooth basis in most squamates (Moody, 1980). New fossil material assigned to the extinct genus *Tinosaurus*, from the earliest Eocene of Dormaal (Belgium), illustrates these ambiguities. The dentition of *Tinosaurus* has always been described as acrodont (Gilmore, 1928; Hecht & Hoffstetter, 1962; Augé, 1990). However, the attachment of its teeth is both lingual and apical, and *Tinosaurus* has a well defined subdental shelf on the dentary as in the members of the Cretaceous family (subfamily?) Priscagamidae (Borsuk-Bialynicka & Moody, 1984; Alifanov, 1989). Despite these facts, we can observe constant features on the dentition of *Tinosaurus*: on the labial surface of the dentary bone there are distinct vertical wear facets located on the bone, between two successive teeth. These facets extend somewhat below the level of the upper edge of the dentary. The presence of occlusal wear indicates that the acrodont teeth are permanent. The bases of acrodont teeth are merged with the lingual surface of the dentary but they do not reach the level of the subdental shelf unlike anterior pleurodont teeth that are present in most species of agamids. Hence, I suggest a definition for the acrodont dentition of lizards as follows: (1) tooth base not fused to the subdental shelf or subdental shelf absent; (2) presence of occlusal wear, mostly on the labial surface of both teeth and bone; (3) Teeth without replacement.

It seems established (Edmund, 1969; Cooper, Poole & Lawson, 1970; Cooper & Poole, 1973) on developmental data, that the acrodont tooth replacement has been derived from the continuous replacement which is regarded as plesiomorphic. Indeed, the contribution of pleurodont teeth to the main cheek series is more significant in early phases of ontogeny of the agamid dentition and decreases with increasing age. Subsequently, these teeth have lost their capacity for replacement in the postnatal stages of ontogeny.

Among lizards, acrodonty occurs only within the Iguania (Agamidae and Chamaeleonidae). The infraorder Iguania is the most primitive group of extant lizards, as shown by its basal position in recent cladograms depicting squamate phylogeny (Estes, de Queiroz & Gauthier, 1988). Acrodont teeth also occur in the Sphenodontia, the sister group to the Squamata (Evans, 1984; Gauthier, Estes & de Queiroz, 1988). Witten (1994) suggests applying the rule of parsimony to members of the Iguania and Sphenodontia. Hence, because of the presumed relationships, acrodonty is apparently primitive for Sphenodontia and Squamata, and, within Squamata, pleurodont teeth would be a derived character. The conflicting evidence resulting from the distribution of characters within taxa and early developmental stage of these characters is not easy to resolve. Some authors (e.g. DeBeer, 1930; Gould, 1977) deny the ontogenetic argument and believe that ontogeny is not a reliable source of information in phylogenetic studies. On the other hand, Nelson (1973) has re-formulated the ontogenetic argument. He considers the ontogenetic transformation of a character (*a-b*) in a species *X* and the lack of transformation in a species *Y* (noted *a-a*). If the normal rules of parsimony are applied to taxa *X* and *Y*, character state '*a*' is plesiomorphic (the most general) and state '*b*' is apomorphic (the least general). Within the Squamata, Acrodonta (Agamidae + Chamaeleonidae) are assumed to show the transformation pleurodont-acrodont (*p-a*) and other lizards are merely pleurodont (noted *p-p*). Sphenodontids are acrodont and an early pleurodont dentition is not observed in the Sphenodontid dentition. However, at least one fossil sphenodontid has anterior pleurodont teeth, the genus *Diphydontosaurus* from the Triassic of U.K. (Whiteside, 1986). The dentary and

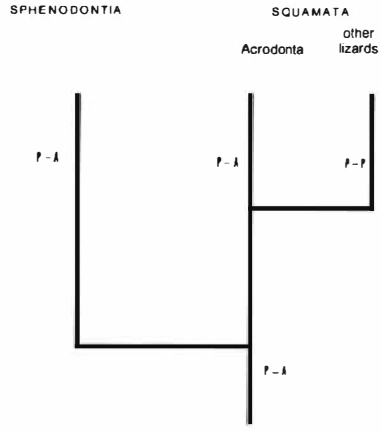

FIG. 1. Alternative interpretations of the ontogenetic transformation in Squamata and Sphenodontia.

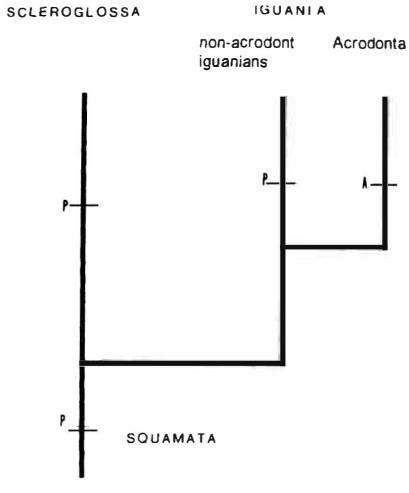

FIG. 2. Distribution of acrodonty (a) and pleurodonty (p) among Squamata. State (p) is more general than state (a).

the maxilla of *Sphenodon* bear anterior successional (replaced) teeth; moreover, those teeth are "canine-like" (Robinson, 1976). *Gephyrosaurus*, first described by Evans (1980) from the lower Jurassic of South Wales is now accepted to be the most primitive relative of the acrodont sphenodonts (Gauthier *et al.*, 1988; Fraser & Benton, 1989) and it is pleurodont. Thus, pleurodont teeth have been present in sphenodontid ancestors and their dentition gives a strong indication of the pleurodont-acrodont transformation (*p-a*). Hence, we admit that the sphenodontids show the transformation (*p-a*) and that this transformation is primitive within Squamata + Sphenodontia (Fig. 1). Moreover, within Squamata, the acrodont lizards (Agamidae + Chamaeleonidae) form a monophyletic taxon along with the Iguanidae, the Iguania (Estes, de Queiroz & Gautier, 1988). Perusal of the distribution of acrodonty and pleurodonty among Squamata leaves no doubt (Fig. 2): the pleurodont dentition is the primitive state for this character.

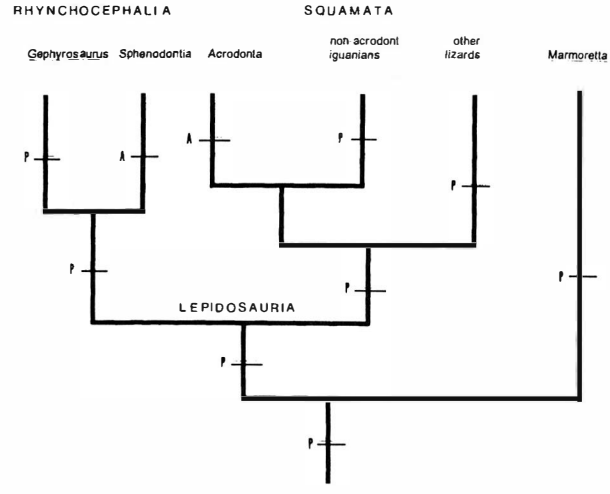

FIG. 3. Distribution of acrodonty (a) and pleurodonty (p) among Lepidosauria + *Marmoretta*.

We may conclude that the transformation pleurodont-acrodont (i.e. acrodonty) seen in the Agamidae and the Chamaeleonidae is a derived condition for Squamata. Outgroup comparisons with the Sphenodontids entirely confirm the polarity of this character.

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SALINITY TOLERANCE AND PREFERENCE IN THE FROG *RANA RUGULOSA* WIEGMANN

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Amphibians are predominantly characteristic of freshwater and damp terrestrial habitats. Early tolerance and physiological studies indicated that amphibians could not survive for more than a few hours in external media more concentrated than about 10 °/$_{oo}$, corresponding to about 30% sea water or 300-350 mOsm l^{-1}, because of osmotic dehydration and diffusional uptake of salt (see Gordon *et al.*, 1961 for review). In the past four decades, a number of anuran species have been discovered living in brackish-water. The most famous of these is the crab-eating frog *Rana cancrivora* which has been extensively studied by physiologists (Gordon *et al.*, 1961; Gordon & Tucker, 1965; Uchiyama *et al.*, 1987, 1990; Uchiyama & Yoshizawa, 1992) and can survive indefinitely in 18 °/$_{oo}$. The frog *Rana rugulosa* is similar in size and appearance to *Rana cancrivora*, while both species live in similar coastal habitats in the northern part of Peninsular Malaysia (K.B. Heang, pers. comm.), and are often collected together by commercial frog hunters. *Rana rugulosa* is a very common frog, widely sold in markets for food; it is not endangered and the bulk of the animals used in the study reported here were held in captivity for a short period before being released to the wild. Firstly, the salinity tolerance of *Rana rugulosa* was investigated for comparison with *Rana cancrivora*. Secondly, the behavioural response of frogs to environmental salinity was assessed. Finally, experiments were conducted to assess the basis of salinity discrimination.

Adult frogs were collected from tidal irrigation channels delivering water to paddy fields near Sungai Petani, Kedah, Malaysia, and used immediately in experiments. At high tide (on 15-9-96) these channels were found to contain water of 5 °/$_{oo}$, though frogs are known to be found in water bodies nearer the sea; comprehensive data for the full range of salinities that they can encounter are unavailable. To test salinity tolerance, 10 frogs were held in each of the following salinities for 72 hr: 0 °/$_{oo}$, 4 °/$_{oo}$, 8 °/$_{oo}$, 16 °/$_{oo}$, 24 °/$_{oo}$ and 32 °/$_{oo}$. Frogs were held in aquaria so that the legs and belly were immersed. At the end of the 72 hr period they were assessed for mortality. To investigate salinity preference, the apparatus shown in Fig. 1 was employed. Made of wood, with a loose-fitting, but light-tight lid, this choice box offered frogs a choice between two media. To conduct an experiment, the two chambers of the box were filled with different media, two frogs were placed in each chamber and the lid applied. After 30 min the lid was opened and the distribution of frogs recorded. The 30 min period was decided upon after pilot trials that demonstrated that no difference in response was evident after longer periods. Each experiment was repeated until a total of 20 frogs had been offered each choice. Between replicate trials, the box was cleaned and the media switched between chambers. Individual frogs were only used once in experiments, and then released to the wild. First, a series of salinities between 8 and 38 °/$_{oo}$ were offered to frogs, the alternative being rain water (0 °/$_{oo}$; ionic concentration unknown). In view of the results obtained, three further choices were offered: 0 °/$_{oo}$ vs. 1000 mOsm NaCl, 0 °/$_{oo}$ vs. 1000 mOsm mannitol, and 1000 mOsm NaCl vs. 1000 mOsm mannitol. These were designed to determine whether *Rana rugulosa* was sensitive to the ionic strength of the outside medium, or to medium osmolarity. During pilot trials, six salinity preference experiments (choice offered; between 0 and 34 °/$_{oo}$) were carried out without a lid on the choice box, allowing direct observation of frog behaviour.

Probit analysis of the salinity tolerance data (Finney, 1971) established that the median lethal salinity (72 hr) for *Rana rugulosa* was 10.2 °/$_{oo}$ (95% confidence limits 8.1 °/$_{oo}$ and 12.0 °/$_{oo}$). Although this frog inhabits broadly similar habitats to *Rana cancrivora*, it is far less tolerant of saline conditions than the latter species, and clearly cannot spend long periods in media more concentrated than 5 °/$_{oo}$. Table 1 displays salinity preference

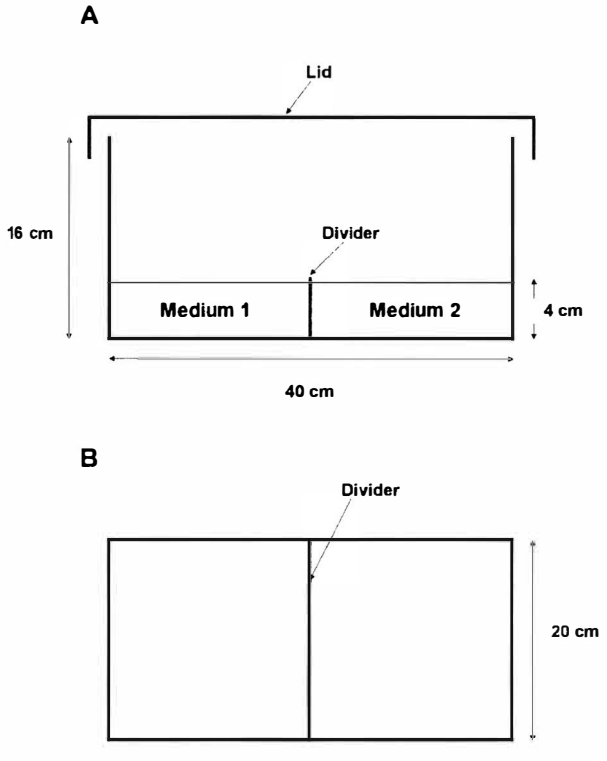

FIG. 1. Apparatus employed in study of salinity choice in *Rana rugulosa*. A, from side. B, plan view.

TABLE 1. Salinity choice in *Rana rugulosa*. 20 different frogs were offered each choice between two media. χ^2_{adj} = χ^2 with Yates' correction for small sample sizes. NS indicates that choice was not statistically significant (P>0.05).

	Available choice			χ^2_{adj}	P
1.	0‰	vs.	38‰		
	17		3	8.45	<0.005
2.	0‰	vs.	36‰		
	16		4	6.05	<0.025
3.	0‰	vs.	34‰	18.05	<0.001
	20		0		
4.	0‰	vs.	32‰	6.05	<0.025
	16		4		
5.	0‰	vs.	28‰		
	16		4	6.05	<0.025
6.	0‰	vs.	26‰		
	13		7	1.25	NS
7.	0‰	vs.	22‰		
	8		12	0.45	NS
8.	0‰	vs.	8‰		
	11		9	0.05	NS
9.	0‰	vs.	1000 mOsm NaCl		
	19		1	14.45	<0.001
10.	0‰	vs.	1000 mOsm mannitol		
	14		6	2.45	NS
11.	1000 mOsm mannitol	vs.	1000 mOsm Na Cl		
	18		2	11.25	<0.001

data for *Rana rugulosa* and it may be seen that the frog has a well developed ability to avoid high salinities (>26‰). Continuous visual observation during pilot trials showed that salinity choice (between 0 and 34‰) started within 20-30 seconds of contact with media and was complete within 3 min. It took place without the frog immersing the snout or head; contact of the medium by the belly and legs was sufficient to initiate choice, and there was no sign of cutaneous transport of fluid to the snout area by 'wicking'. The data for choices involving 1000 mOsm mannitol and 1000 mOsm NaCl were illuminating. These media are both approximately isosmotic with sea water (1000 mOsm≡ 31‰; Rankin & Davenport, 1981). However, while 1000 mOsm NaCl was avoided to a highly significant extent (when the alternative was fresh water), 1000 mOsm mannitol was not. In addition, when frogs were offerred a choice between 1000 mOsm mannitol and 1000 mOsm NaCl, they showed pronounced avoidance of the salt solution, even though both solutions will lead to similar rates of osmotic dehydration. Taken together these data indicate that salinity choice behaviour by the frogs is determined by ionic concentrations, not by osmolarities.

It is evident that *Rana rugulosa* does not have the tolerance of salinity exhibited by *Rana cancrivora*. However, it does have the ability to recognize and escape from deleterious salinities, a useful attribute in a mobile species inhabiting environments where some bodies of water will be more saline than others. Salinity discrimination is by cutaneous response, and is rapid, presumably because of the high permeability of frog skin to salts and water.

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SUBSTRATE SHIFTS IN A POPULATION OF STRIPED PLATEAU LIZARDS, *SCELOPORUS VIRGATUS*

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Lizards may alter their orientation to the sun, or their location relative to the sun (e.g. shuttling between sun and shade) during the day to maintain a nearly constant body temperature (Waldschmidt, 1980; Middendorf & Simon, 1988; Martin, López, Carrascal & Salvador, 1995). Other lizards change habitats on a seasonal basis. For example, Galapagos land iguanas (*Conolophus pallidus*) use a cliff face (protected from wind) in the cool season and a plateau (windier) in the hot season (Christian, Tracy & Porter, 1983). Some of these shifts involve changing the substrate or perch used (Adolph, 1990; Castilla & Bauwens, 1991) or even changing the amount of incident solar radiation (Carrascal & Díaz, 1989; Díaz, 1992; Martin *et al.*, 1995). At a larger spatial scale, shifts can involve movements between broad habitat types (Christian *et al.*, 1983; Buttemer & Dawson, 1993). In this note, I consider whether substrate use in a population of the striped plateau lizard, *Sceloporus virgatus*, shifts across the activity season. In addition, I determine if there are similar shifts in habitat and slope use, and if striped plateau lizards change their use of sunny and shaded microhabitats during the activity season.

The study site in the Chiricahua Mountains of SE Arizona (Cochise County) (see Smith, 1996*a*) was a 1.2 km stretch of an east to west creek-bed with north- and south-facing slopes. In addition, two habitat types existed on the study site: a woods habitat and a slide habitat. The slide habitats were open with few trees (30% of the study area), whereas the woods habitat had several trees and relatively closed canopies (70% of the study area). Mean monthly temperatures were obtained from the Southwestern Research Station (approximately 1.5 km from the study area).

I made observations on lizard habitat and substrate use from June to August, 1992, and from April to July, 1993 and 1994. I recorded the slope (north-facing or south-facing), habitat (woods or slide), and substrate (rock, log or ground) on which an individual was first observed, as well as whether the individual was first seen in full sun, a sun-shade mosaic, or full shade. Lizards were individually marked as they were also part of a mark-recapture study (Smith, 1996*b*).

Because I often had several observations per individual, to maintain independence of observations I randomly selected a single observation per individual per year to use in the analysis. This is particularly important because individual *S. virgatus* appear to have different preferences for slopes, habitats, and substrates (Smith, 1996*a*). To examine shifts in substrate, habitat, slope use, and sun/shade use, I broke down all observations by month (e.g. June, July, August for 1992; April, May, June, July for 1993 and 1994). Each year was ana-

TABLE 1. Monthly use of slopes (proportion on north-facing slopes), habitats (proportion in woods habitat), substrates (proportion on rock substrate), and microhabitats (proportion in full sun) by *Sceloporus virgatus* in the Chiricahua Mountains of SE Arizona. Total number of individuals per month given in parentheses. Statistics reported in text conducted on raw scores, not on proportions given here. * indicates that the shift was significant at an α-value of 0.0167.

	April	May	June	July	August
Slope					
1992	—	—	0.43 (122)	0.48 (101)	0.40 (37)
1993	0.44 (85)	0.34 (91)	0.57 (86)	0.49 (45)	—
1994	0.35 (60)	0.48 (128)	0.48 (73)	0.52 (27)	—
Habitat					
1992	—	—	0.68 (122)	0.67 (101)	0.65 (37)
1993	0.70 (85)	0.72 (91)	0.70 (86)	0.58 (45)	—
1994	0.79 (61)	0.68 (127)	0.63 (71)	0.70 (27)	—
Substrate					
1992*	—	—	0.49 (120)	0.25 (101)	0.16 (37)
1993*	0.72 (85)	0.59 (90)	0.49 (84)	0.49 (45)	—
1994*	0.80 (61)	0.56 (128)	0.49 (72)	0.48 (25)	—
Microhabitat					
1992	—	—	0.38 (98)	0.31 (84)	0.57 (28)
1993*	0.63 (78)	0.49 (67)	0.18 (83)	0.28 (29)	—
1994*	0.71 (58)	0.41 (113)	0.16 (62)	0.09 (23)	—

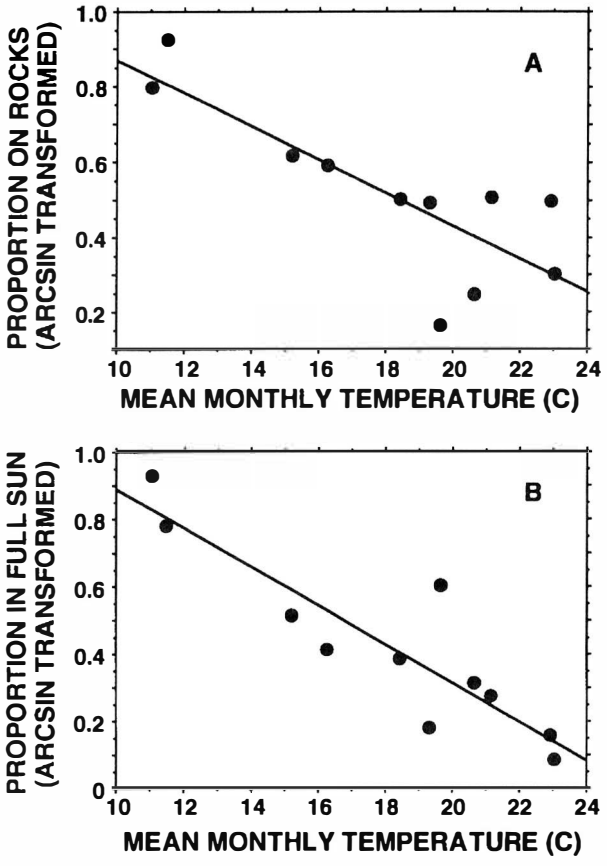

FIG. 1. (A) The inverse relationship between mean monthly temperature and the proportion (arcsine transformed) of *Sceloporus virgatus* using rock substrates. See text for statistics and equation. (B) The inverse relationship between mean monthly temperature and the proportion (arcsine transformed) of *Sceloporus virgatus* using sunny microhabitats. See text for statistics and equations.

lysed separately. Preliminary analyses of males and females separately found no significant differences between them ($P > 0.05$), thus males and females were pooled for this study. I used chi-square tests to compare lizard distributions between months within a year. I used a corrected α-value of 0.05/3 = 0.0167 to adjust for multiple tests on each data set.

In all three years, habitat use did not shift between months (Table 1; 1992: df = 2, $\chi^2 = 0.13$, $P = 0.94$; 1993: df = 3, $\chi^2 = 3.31$, $P = 0.35$; 1994: df = 3, $\chi^2 = 3.86$, $P = 0.28$). In 1992 and 1994, monthly slope use did not differ (Table 1; 1992: df = 2, $\chi^2 = 0.92$, $P = 0.63$; 1994: df = 3, $\chi^2 = 3.71$, $P = 0.29$). In 1993, there was a nearly statistically significant shift, with fewer individuals using north-facing slopes than expected in May (Table 1; df = 3, $\chi^2 = 9.71$, $P = 0.02$).

Shifts in substrate use were apparent and significant in all three years of the study (Table 1; 1992: df = 4, $\chi^2 = 25.66$, $P<0.0001$; 1993: df = 6, $\chi^2 = 25.44$, $P=0.0003$; 1994: df = 6, $\chi^2 = 21.37$, $P = 0.002$). In all years, the use of rock substrates decreased, while the use of ground substrates – and to some extent log substrates – increased as the activity season progressed. The proportional use of rock substrates (arcsine transformed) decreased linearly with mean monthly temperatures (Fig. 1A; $n = 11$, $r^2 = 0.65$, $P = 0.004$; y = 1.31 - 0.044x).

Monthly changes in the use of sun, sun/shade mosaic, and shade microhabitats were not significant in 1992, but highly significant in 1993 and 1994 (Table 1; 1992: df = 4, $\chi^2 = 9.60$, $P = 0.048$; 1993: df = 6, $\chi^2 = 41.8$, $P < 0.0001$; 1994: df = 6, $\chi^2 = 48.7$, $P < 0.0001$). Individuals tended to use sunny microhabitats in April and May, and shaded microhabitats in June and July. The proportional use of sunny microhabitats (arcsine transformed) was inversely related to the mean monthly temperature (Fig. 1B; $N = 11$, $r^2 = 0.80$, $P = 0.0002$; y = 1.46 - 0.057x).

Sceloporus virgatus show shifts in substrate and microhabitat use (i.e. amount of sun), but not in habitat and slope use. The evidence presented here suggests that substrate and microhabitat shifts are related to thermoregulation. As environmental temperatures rise there is a concomitant decrease in the use of rocks and sunny microhabitats. Different perches and microhabitats generally provide different thermal and microclimatic conditions (Bakken, 1989), and thus the *S. virgatus* in this population may change their substrate and microhabitat use to maintain a constant body temperature throughout the activity season. Indeed, *S. virgatus* in the Chiricahua Mountains maintain a relatively constant body temperature despite widely varying air temperatures (Smith & Ballinger, 1994). Using rocks during the warmer months may cause *S. virgatus* to have body temperatures higher than the preferred temperature, as individual *S. virgatus* on rocks tend to have higher body temperatures than individuals on ground substrates (Smith & Ballinger, 1994). Therefore, the decrease in the use of rock substrates is consistent with a thermoregulatory function. The shift away from sunny microhabitats is also consistent with a thermoregulatory explanation, as has been seen in other lizards (Van Damme, Bauwens & Verheyen, 1987; Carrascal & Díaz, 1989; Castilla & Bauwens, 1991). Similar shifts on an hourly basis (i.e. use sunny substrates less during the heat of the day) occur in other lizard species (e.g. Waldschmidt, 1980).

My results, while strongly suggesting a thermoregulatory explanation for the observed shifts, do not exclude the possibility that other environmental factors are driving the observed substrate and microhabitat shifts. First, the shifts may result from the lizards following their insect prey as they shift microhabitats or substrates. In this case, it would be the insects that are thermoregulating and the lizards who are following along. I do not believe this is as likely as thermoregulation to explain the shift because of the scale of the shifts and the foraging behaviour of *S. virgatus*. The shifts observed here occur over a scale of 1-2 m, much smaller than the home range of these lizards (Smith, 1995), and *S. virgatus* are sit-and-wait type foragers

that forage from a perch, and may run through other substrates or microhabitats to capture prey (*pers. obs.*). Thus, the food explanation might be more likely to explain a habitat or slope shift than a substrate of microhabitat shift. Another possibility is that these are shifts associated with mating behaviour or with females carrying eggs. While possible, the fact that males and females did not differ in their shifts in substrate or microhabitat (preliminary results mentioned above), suggests that the sexes were not behaving differently, at least as far as substrate and microhabitat use were concerned. Other non-thermoregulatory explanations exist, such as the shifts accompanying changes in anti-predator behavior, but no data exist to evaluate them.

In conclusion, *S. virgatus* alter their substrate and microhabitat (i.e. sunny vs shaded microhabitats) use throughout their activity season. These shifts appear to be closely linked to environmental temperatures and are likely tied to thermoregulation (but other factors may be involved: see above). Ultimately, the observed shifts may increase daily and seasonal activity periods with ramifications for the lizard's life history and ecology.

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THE USE OF IMITATION SAND LIZARDS TO ASSESS THE ACCURACY OF VISUAL SURVEYING TECHNIQUES

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Assessment of sand lizard, *Lacerta agilis*, populations is a prerequisite for their conservation and provides a sound basis for management. The problems associated with surveying reptiles are well documented; approaches include mark-recapture, refuges (or cover boards) and direct observation (Gent, 1994; Reading, 1996; Sutherland, 1996).

Direct, or visual, observation is a widely used approach although different methodologies may be adopted. Corbett & Moulton (1996) undertook a comparative study in order to determine the number of lizards observed when using 'directed' and 'straight-line' transects. Experienced surveyors can conduct surveys by a 'directed' transect, defined as " ... a route..., embracing features known to be attractive to reptiles and allowing ease of movement with minimal disturbance to fauna and flora " (Corbett & Moulton, 1996). An alternative approach is to adopt a simple 'straight-line' transect, which is easy to repeat in a standardized manner and can allow those with less experience to undertake surveys. Directed transects are 'biased' in that they are dependent on the preferences of the surveyor, whilst straight line transects avoid this.

This study compares the efficiency of 'directed' and 'straight-line' transects in assessing sand lizard populations when undertaken by surveyors with experience ranging from 'novice' to 'professional'. Surveyors searched for 'populations' of sand lizards, represented by plastic models of adult males, on heathland sites. Models were painted to represent the cryptic colouration described by Stafford (1989) and were of similar size and physical appearance to real lizards.

Transects were located along linear experimental areas which contained features associated with the occurrence of sand lizards. Each model was located in a position representative of sand lizard behaviour (Gent, 1994; NCC, 1983; Prestt, Cooke & Corbett, 1974) in a basking site defined by Inns (1995) as " a pool of sunlight deep in the vegetation or on the sunny edge of dense vegetation ". Surveys were undertaken at three heathland sites supporting reptile populations, selected carefully for similarity, and comprising mature stands of dry heath low scrub (20 to 40 years old), dominated by *Calluna vulgaris* and *Erica cinerea*. The sites had a southerly, south-westerly, or westerly aspect; were unshaded, and had sand features considered attractive to sand lizards. Sites were pre-selected as those considered typical habitats for sand lizards and surveys were conducted under appropriate weather conditions, with temperatures in the range 11 to 18°C during partially sunny or hazy weather with little or no wind (Inns, 1995).

Fifteen surveyors were identified as 'novice', 'experienced' or 'professional' according to their surveying skill, each group containing five surveyors. 'Novice' indicated that surveyors had no prior experience of reptile surveying but, prior to the experiment were briefed on sand lizard behaviour and survey methodology. 'Experienced' surveyors consisted primarily of British Herpetological Society volunteers, and had one or two seasons of surveying experience. 'Professional' surveyors were those with considerable experience of surveying, exceeding two surveying seasons.

Each surveyor was required to walk a 'straight-line' and a 'directed' transect, the order being assigned randomly. In order to allow comparison of the two

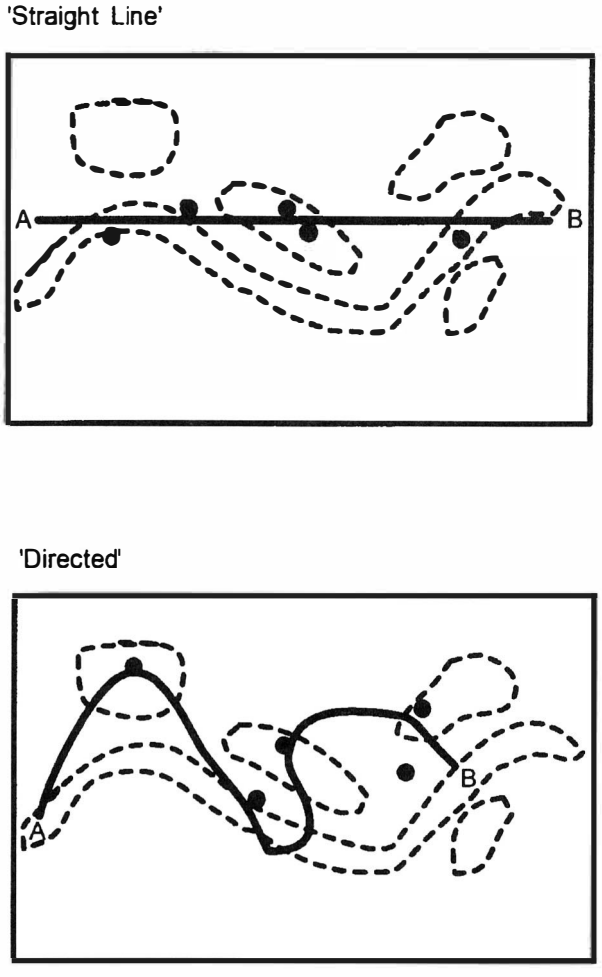

FIG. 1. Schematic diagrams of 'straight line' (visually searching 4 m either side of transect) and 'directed' (unrestricted surveying) transects. The survey area included features such as sandy areas (dotted areas). Models were located so that, in each case, five models could be observed during the 20 min traverse of the transect.

techniques, care was taken to ensure that sampling effort was equal, and was standardized by limiting transect length and restricting the the time taken to conduct each survey to 20 min. Straight-line transects (100 m) were undertaken between two previously marked points (Fig. 1). Each surveyor was instructed to observe any sand lizards sighted within a 4 m band either side of the transect. A directed transect was searched between two points 75 m apart. Surveyors were allowed to deviate from a straight line in order to inspect areas considered to be potential basking sites (Fig. 1).

Five models (to represent a realistic number of individuals) were placed within the boundaries of the transect search areas in basking sites defined above, and surveyors were not aware of the number or location of models. In all cases, a surveyor could have observed all five models in the time given to search each transect.

As well as colouration, cues such as movement and noise may also be used to locate lizards (Inns, 1995). Although this study was designed to assess visual observation, disturbance by the surveyor was also represented and recorded. When a model was observed, surveyors recorded whether the model had been observed within, or beyond, a 2.5 m distance. The distance of 2.5 m was somewhat arbitrary, but was set to represent a proximity which would be likely to cause disturbance of the lizard. The number of sightings from a distance exceeding 2.5 m and the number of total sightings were calculated from each group. Data were analysed by calculating summary statistics and by ANOVA, using a two-factor mixed design with one within subjects factor (Kinnear & Gray, 1994), for both total sightings and sightings exceeding 2.5 m.

Sightings from distances exceeding 2.5m were not significantly different for either method ($F_{1,12} = 3.4$, $P<0.05$) or level of expertise ($F_{2,12} = 2.7$, $P<0.05$). Inspection of the data indicated no trend for the mean numbers of sightings with respect to expertise for the straight-line transect, whilst the level of expertise appeared to be related to the mean number of sightings for directed transects, although this relationship was non-significant (Fig. 2).

Total sightings were significantly different for both method ($F_{1,12} = 19.1$, $P<0.01$) and level of expertise ($F_{2,12} = 14.0$, $P<0.01$). A significant interaction between method and the level of expertise was observed ($F_{2,12} = 30.4$, $P<0.01$). These results show that whilst the mean number of sightings clearly increased with the level of surveyor experience for the directed method, no pattern was discernible for straight-line transects, indicating that the level of experience did not influence sightings when this methodology was used (Fig. 2).

The proportion of models sighted increased with surveyor expertise from distances exceeding 2.5 m, and total sightings for directed transects, reaching 0.32 and 0.96 respectively for professional surveyors, whilst the proportion of sightings using straight-line transects were with the exception of novice observers generally lower (Fig. 2).

The results demonstrate that data collected from visual surveys is dependent upon both methodology and the level of surveyor expertise. Although five lizards could, in principle, have been seen using either method, numbers recorded using the directed transects were higher than those recorded using the straight-line transect for experienced and professional surveyors, whilst the reverse was true for novices. This suggests that surveyors with experience are able to use their understanding of reptile behaviour to locate areas likely to have lizards present with directed transects. However, lizards were placed in locations considered to be attractive and so this result is unsurprising. Novices were poor at surveying using directed methodology for this very reason; they did not have the expertise to find these 'preferred' locations. However, when the straight-line transect was adopted, results were not demonstrably dependent on expertise. Directed transects, therefore may maximize sightings when undertaken by expert surveyors, but straight-line transects have the benefit of not being expertise-dependent and thus not subject to bias. Directed transects are useful in terms of assessing presence/absence when undertaken by experienced surveyors, whereas straight-line transects are a standardized, repeatable technique which is expertise-independent and can be used to demonstrate, for example, annual changes in numbers more effectively than the directed methodology.

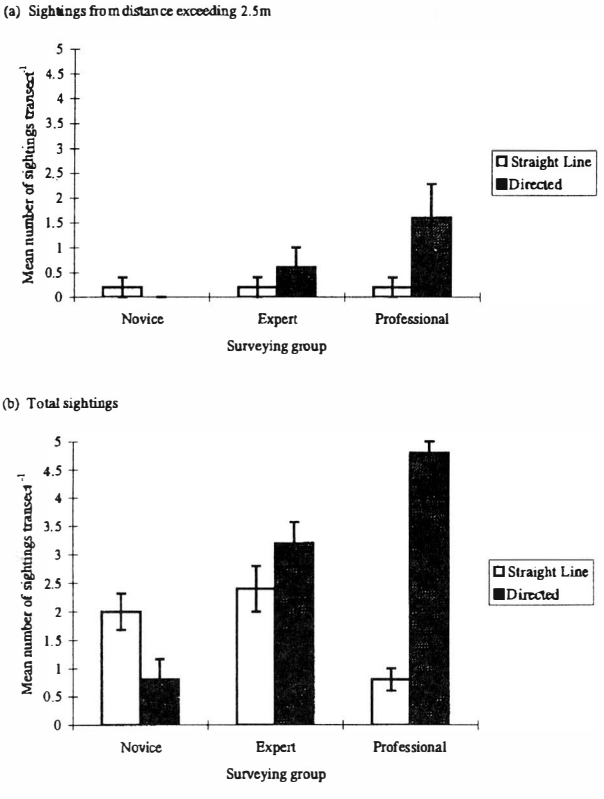

FIG. 2. Mean number of sightings (±SE) of sand lizard models by surveyors of novice, expert and professional experience using straight line and directed transects.

The positioning of straight line transects needs careful consideration. Repeated transects located at random may be used to estimate density (Buckland *et al.*, 1993), whilst if transect location is pre-determined as in this study, features suitable for sand lizards may be included. If surveying is undertaken by those with little experience, adequate surveying may be possible with appropriate guidance and training if a pre-marked route is set out by an experienced herpetologist (N. Moulton, pers. comm.). Other considerations may also influence the type of methodology adopted. Corbett & Tamarind (1979) stated that rigid adherence to straight-line transects could cause damage to dense heathland stands which may lead to changes in the successional status of heath (Burden & Randerson, 1972). However, straight-line transect methodology could include some allowance for deviation from the line in order to reduce damage.

The proximity to lizards is an important factor influencing efficiency. Although the distance of 2.5 m was arbitrary, it does suggest that factors such as disturbance or a surveyor's inability to spot lizards at a distance could compromise the survey results; professional surveyors were 96% efficient for total counts, but only 32% efficient for sightings at a distance exceeding 2.5 m. Any standardized methodology should account for factors such as disturbance, particularly if it is anticipated that the method will be adopted by beginners (the novice group, using directed transects, were unable to locate any lizards at a distance exceeding 2.5 m, and only 16% in total). By retreating and then returning after 10 to 15 mins, a lizard may return to its basking position following disturbance and so a standardized methodology could include surveyors returning to features. Stealth and a good field-eye are required because of the mobility, shyness and cryptic colouration of this species (Sutherland, 1996).

The use of plastic models allows a degree of quantification which is difficult to obtain when observing real lizard populations. The advantage of this approach is that repeat surveys are possible; it is known that each surveyor will encounter the same distribution and number of 'lizards'. This study, however, assumed that the locations of lizards expected by herpetologists truly represents their distribution and further study would be needed to investigate the effects of expertise and transect type fully. Further study could locate lizards randomly within search areas to determine whether the ability of experienced surveyors to locate lizards is due to a refined 'search image' or whether they simply are able to locate 'suitable' sites. The methodology could also be extended to other reptiles and could, perhaps, be developed to compare survey efficiency under different habitat types and prevailing weather conditions, or the efficiency of sighting lizards when these are located within different habitat features.

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SELECTED BODY TEMPERATURES OF FOUR LACERTID LIZARDS FROM THE CANARY ISLANDS

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Among the most conspicuous aspects of lizard biology are the interactions between the animals and their thermal environments (Huey & Stevenson, 1979; Avery, 1982). A commonly used variable that may contribute to the characterization of the thermal biology of a species or a population is the selected body temperature (T_b), or the set point range (Pough & Gans, 1982; Hertz, Huey & Stevenson, 1993), which is a measure of the preference zone of body temperatures maintained by behavioural thermoregulation in a thermal gradient, an environment without ecological costs (Huey & Slatkin, 1976) or physiological constraints (Porter & Gates, 1969). When direct measures of physiological performance are unavailable, selected temperatures are the most meaningful measures in the thermal ecology of a given species (Huey, 1982).

The genus *Gallotia* (Sauria: Lacertidae) is endemic to the Canary Islands (Arnold, 1973). According to the latest taxonomic revision, it comprises five species distributed over the seven main islands (López-Jurado, Mateo & Guillaume, 1996). There is some information on the distribution and some aspects of the differentiation of *Gallotia* in the Canary Islands (Thorpe, 1985; López-Jurado, *et al.*, 1986). There is descriptive information about the present-day population and basic general information on distribution and general natural history of the poorly known Giant lizard of El Hierro, *Gallotia simonyi* (Machado, 1985 and references therein). There are also a few behavioural studies on *Gallotia* (Böhme & Bischoff, 1976; Molina-Borja, 1981). However, the only available information about the thermal biology of *Gallotia* is provided by Báez (1985), in a short study of *G. galloti eisentrauti*, and by (Díaz, 1994) in a study of the western Canarian lizard *G. galloti galloti*. Both of these subspecies are endemic to the island of Tenerife.

In this preliminary study we provide the first basic information on selected body temperatures for four species of *Gallotia*: a large species from the island of Gran Canaria, *Gallotia stehlini*; a smaller species from the island of Lanzarote (although there is a population in Gran Canaria), *Gallotia atlantica*; and two endemic species from the island of El Hierro: the common small *Gallotia caesaris*, and the endangered Giant lizard of El Hierro, *Gallotia simonyi*, a species limited to a relict population which is the subject of a recovery plan based on captive breeding (Pérez-Mellado, *et al.*, 1997).

Gallotia stehlini and *G. atlantica* were tested in the facilities of the Centro de Investigaciones Herpetológicas between 12-22 June 1995 in Galdar, Gran Canaria. Individuals of *G. stehlini* were captured in the vicinity of the testing site (28°7.5' N - 15°40.9' W), and *G. atlantica* were captured in Malpaís de la Corona, Lanzarote Island (29°14.5' N - 13°30' W). Lizards from El Hierro were tested in the facilities of the Centro de Recuperación del Lagarto Gigante de El Hierro (CRLGEH), in Guinea, El Hierro (27°45.4' N - 17°59' W) from 4-29 April 1995. Juveniles of *G. simonyi* were tested between 10-12 January 1996, four months after hatching in captivity. The giant Hierro lizards tested were from the captive breeding stock of the CRLGEH, and *G. caesaris* were collected in the immediate vicinity of the premises. All the lizards collected in the wild were kept in captivity for two weeks to a month prior to testing to allow them to adjust to captive condition. Food and water were provided *ad libitum* to experimental animals.

Lizards were tested in 150 x 50 x 50 cm glass walled thermal gradient chambers floored with gravel. A heat source (250 W infra-red bulb) was suspended at one end, creating a gradient of air temperatures ranging from 17 to 57 °C. In El Hierro, the experiments were carried out mainly during the morning hours (09.00-14.00 hrs) or when air temperatures in the room were cool. In Gran Canaria the tests were carried out between 09.00-18.00 hrs, in an air-conditioned room to ensure that the gradients were not too hot. The cloacal temperature of the tested animals was taken with a Miller & Weber thermometer (0.2°C precision). Three measurements were obtained from each individual, one, two, and three hours after it was placed in the thermal gradient chamber. All lizards captured in the wild were returned to their capture sites at the end of experiments. A maximum of four small-sized individuals or two large-sized lizards were used synchronously. When more than a single individual was tested synchronously the individuals used were selected from similar size and sex classes to minimize agonistic interactions, which were absent in all trials.

For each species and class, we give the grand mean of the averages of individual T_b (see Huey, Niewiarowski, Kaufmann & Herron, 1989 for a similar approach). We also provide set point ranges (T_{set}, Table 1), estimated as the central 80% of all T_b selected in the laboratory (Hertz *et al.*, 1993). All individual measurements (three per individual) were included to calculate T_{set}. We did not detect significant differences in average T_b between classes (males, females, and juveniles) within three species (Table 1, one-way ANOVA, *G. atlantica*, $F = 1.06$, $P = 0.35$; *G. simonyi*, $F = 2.80$. $P =$

TABLE 1. Mean, standard deviation (SD), range and set point (T_{set}) for selected temperature (T_b); and mean, standard deviation and range of snout-vent length (SVL).

	Gallotia caesaris			*Gallotia atlantica*		
	male	female	juvenile	male	female	juvenile
T_b (C)	35.3	35.7	34.3	33.8	32.9	33.0
SD	1.85	1.46	1.36	1.63	3.36	1.67
Range	26.0-40.5	26.6-40.0	21.8-39.4	24.5-37.5	24.2-38.1	23.6-37.1
T_{set} (C)	32.1-38.0	33.6-38.1	32.5-37.0	30.5-36.4	26.4-36.3	28.6-36.4
SVL (mm)	68.6	66.1	52.1	88.6	70.8	61.2
SD	6.47	5.00	4.76	7.90	5.04	5.54
Range	58-81	58-75	42-61	104-74.5	78-65	66-51
N	33	21	18	25	7	14
	Gallotia simonyi			*Gallotia stehlini*		
	male	female	juvenile	male	female	juvenile
T_b (C)	35.2	35.6	36.3	33.7	33.5	34.6
SD	1.74	1.35	1.36	1.62	1.96	1.41
Range	26.0-40.0	29.6-39.4	27.0-39.0	27.5-38.3	27.1-39.0	30.4-36.6
T_{set} (C)	32.4-38.3	33.2-37.9	35.0-38.3	30.8-36.4	30.0-36.9	31.7-36.5
SVL (mm)	198.6	182.2	61.3	189.6	155.6	103.4
SD	21.44	12.77	6.78	27.78	18.38	26.02
Range	226-144	204-143	80-52	244-150	195-132	140-75
N	31	24	17	21	12	8

0.07; *G. stehlini*, $F = 1.14$; $P = 0.33$). Only the results for *G. caesaris* yielded significant differences between classes (One-way ANOVA, $F = 3.60$, $P = 0.03$), and the significance was due only to the difference between the most (females) and the least thermophylic class (juveniles), the rest of the pairwise comparisons being non-significant (Tukey-Kramer HSD test). In Gran Canaria, the selected temperatures in the tests performed in the afternoon (14.00-18.00 hrs) did not differ significantly from those obtained in the morning (09.00-14.00 hrs, $t = -1.37$, $P = 0.17$).

A multifactor ANOVA was set up to compare three effects: "island" (the two species present in Gran Canaria *vs.* the two species endemic to El Hierro), "adult body size" (small species *vs.* species reaching larger sizes), and "class" (male, female, juvenile). The "island" effect appears to be highly significant, indicating that the lizards from El Hierro (*G. simonyi* and *G. caesaris*) have significantly higher selected temperatures, than the species from Gran Canaria ($F = 53.95$, $P = 0.001$). The selected temperatures of species reaching large adult sizes (*G. stehlini* and *G. simonyi*) were also significantly higher that those of the species not reaching large adult sizes (*G. atlantica* and *G. caesaris*; $F = 6.77$, $P = 0.01$). Finally, the effect of class (male, female, juvenile) was not significant ($F = 1.56$, $P = 0.88$).

In order to determine whether preferred temperatures changed with individual size within each species, the correlations between selected body temperatures (T_b) and body size (SVL) were studied. The two species that reach larger adult sizes yielded significant correlations (*G. simonyi*: $n = 72$, $r = 0.288$, $P = 0.01$; *G. stehlini*: $n = 40$, $r = 0.372$, $P = 0.01$). However, this effect may be an artifact. Actually, if the data for the juveniles are excluded, the correlations are not significant (*G. simonyi*: $n = 55$, $r = 0.134$, $P = 0.32$; *G. stehlini*: $n = 32$, $r = 0.30$, $P = 0.094$). On the other hand, the smaller species showed positive correlations between SVL and T_b, although the relationship was only significant in the species from El Hierro (*G. atlantica*: $n = 46$, $r = 0.234$, $P = 0.11$; *G. caesaris*: $n = 72$, $r = 0.322$, $P = 0.001$).

We detected significant differences in selected temperatures between islands. This fact could reflect a different thermal regime in these islands (or between a western Island: El Hierro, and two eastern islands: Gran Canaria and Lanzarote) which may act as a selective pressure on thermal preferences of lizards (see Avery, 1982 and references therein). Alternatively, differences in thermal preferences could result from differences in times of activity (Huey & Bennett, 1987). Crepuscular and nocturnal activity has been recorded in *G. galloti* and *G. stehlini* (Böhme *et al.*, 1985; Böhme, pers. comm.) but not in *G. simonyi*. Thus, different thermal preferences could also be linked with different activity cycles, maximizing activity times in each species (Huey & Slatkin, 1976; Huey, 1982).

It is clear that much more research is needed to test these hypotheses, especially on operative temperatures (Bakken, 1992) available in the natural habitats of each

species, and on thermal dependence of digestive efficiency and sprint performance (Huey, 1982). In any case, knowledge of thermal optima is also relevant for the correct design of a captive breeding program, the key factor in the recovery plan of *G. simonyi* (Pérez-Mellado *et al.*, 1997).

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BOOK REVIEWS

Amphibians and Reptiles of North Africa. H. Hermann Schleich, Werner Kästle and Klaus Kabisch. (1996). 630 pp., 63 colour plates. Koeltz Scientific Books, Koenigstein, Germany. DM220 (cloth).

With works on the amphibians and reptiles of Europe, including countries bordering the northern Mediterranean, available for many years now (e.g. Arnold, Burton & Ovenden, 1978), an authoritative work on species of the lands bordering the southern Mediterranean has long been overdue. In this work we have a volume for which herpetologists have long been waiting. It covers a wide range of species, many of which are poorly-known, and represents a task that some herpetologists would have found daunting.

Following a foreword by Wolfgang Böhme which is essentially a review anyway, and a self-effacing preface by the authors, an informative introduction outlines the scope of the book and difficulties regarding systematics and geographical distribution. It draws attention to the relative lack of information on many of the species found in North Africa. It is curious, and contrary to what has become customary in the last decade or two, that common names of species begin with a capital letter. A check-list of the amphibians and reptiles of North Africa then sets the stage. North Africa is defined geographically by the political boundaries making up Morocco, Algeria and Tunisia (the Maghreb), and also Libya. Species restricted to Egypt, including those tropical forms entering Egypt by the Nile valley, are indicated in the check list, which is thus given a look of northern Africa rather than traditional North Africa *per se.* It is to my mind a wise decision to exclude these tropical invaders from the specialist treatment.

The book therefore provides a thorough coverage for all of the species found in geo-political North African countries, which include a major part of the Sahara Desert. Climatic and vegetational characteristics of the region are then addressed, followed by zoogeographic affinities, endemism and disjunct distributions. A series of approximately N–S. transects across North Africa give the altitude-vegetational distribution of species occurring in the regions. One section on ecological aspects covers the different types of habitat (or 'biotopes') occupied by each species, tabulated in a way similar to Lambert (1984) (quoted but not included with the references list at the end of the book), temperature and behavioural adaptations, reproductive patterns, trophic complexes (usefully emphasizing the importance of lizards as a link between invertebrates and predators higher up food chains), herpetofaunal communities, and the impact of man. This is followed by a systematic treatment of each species, starting with the Amphibia. A key sorts out the different amphibian and reptile classes, and then three others commendably identify amphibian species from eggs, larvae and adults. There are helpful line drawings in a wide left margin to illustrate or elaborate on what is said in the text under each species description, which follows a fairly traditional handbook/fieldguide style. The 63 coloured plates of species and habitat (three photos per plate) are presented as a block between the chelonians and lizards of the Reptilia. Each species is given thorough treatment under the headings of etymology, identification, ecology and general behaviour, reproduction, geographic range, systematics (or subspecies) and references. The book ends with a section listing the species of Egypt, with identification key, and appendices giving scientific terms, geographic and topological terms in Arabic and Berber, and a list of bird and mammalian predators of amphibians and reptiles in North Africa. There is then an index of Latin names of species, common names in English, French and German, and finally, literature.

With regard to the Amphibia, although I am not a specialist, I could not find anything that was inaccurate or plainly incorrect for species under, say, the genus *Bufo*; in fact some earlier misconceptions of mine were ironed-out. Among the Reptilia, I took a closer look at *Testudo graeca,* in which I have more experience. I was surprised not to see included with the key (p. 148) the single pair of dark markings on the anterior edge of the abdominal scutes in *T. (Pseudotestudo) kleinmanni* as a character separating it from *T. graeca*, and I query whether the shell colouration characters indicated (fig. 149/1) are valid for separating out *T. g. terrestris* as a subspecies in North Africa. The authors have retained their own views on this. I was pleased to note that for the time being they have not followed the newly named tortoise species in Algeria and Tunisia, and I agree that the whole taxonomy of *Testudo graeca* requires genetic clarification (p. 151). I did expect to see Loveridge & Williams (1957) and, on a more subjective note, Lambert (1982) included as references for this species; the former is, however, quoted for other chelonians and included with the list of references at the end of the work. Among the plates (41), one cannot help noticing that *Leptotyphlops macrorhynchus* (117) is placed under Typhlopidae, and not Leptotyphlopidae, where it is correctly placed in the text (p. 475). For *Uromastyx*, is *acanthinura* (pp. 298-311) a more recent spelling than *acanthinurus*, as given in, say, Joger & Lambert (1996)?

Scincus albifasciatus Boulenger, 1890 (p. 363), with a range in Sénégal and the southern half of Mauritania (not Mauritanica), is now surely generally accepted as a species separate from *S. scincus.* Among these detailed kinds of comments, one might also like to have seen under *Acanthodactylus boskianus* (p. 380), since this is available, additional information on food (Robson & Lambert, 1980), and for *Acanthodactylus dumerili* (one

of the *A. scutellatus* group), some more information on ecology, with a further reference on the subject, Cissé & Karns (1977). But perhaps one cannot cover everything. The purist will undoubtedly find further differences concerning relative minutiae of this kind, and there could have been slight touching-up on the English all through the work. However, all in all, the authors have "grabbed the bull by the horns", taken up a difficult challenge, and produced a useful book of reference, which is generally authoritative and most certainly thorough and comprehensive. The herpetologist visiting North Africa and traversing the land from HM King Hassan II's Morocco to Col. Al-Gaddafi's Libya will find the work an invaluable companion – I wish I had had it when completing in stages such a journey along this route, and including Egypt, in the 1960's and 70's!

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Herpetology of Japan and Adjacent Territory. Leonhard Stejneger. (1996). 620 pp. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA (in co-operation with the Herpetological Society of Japan). (Facsimile Reprints in Herpetology). $58.00 (cloth).

Although first published in 1907 (Bulletin 58. Smithsonian Institution, United States National Museum. Government Printing Office, Washington.), this remains the only comprehensive English language work on the reptiles and amphibians of Japan. Covering, in addition, Taiwan, Korea, Manchuria, adjacent coastal China and eastern-most Siberia, it has for nine decades been an invaluable source for students of Russian, Chinese and Korean, as well as Japanese, herpetology. The passage of time has, however, meant that usable copies of the original volume have become increasingly difficult to obtain, and so the decision by SSAR to produce this facsimile is to be welcomed.

The value of the 1996 edition is enhanced by the inclusion of a twenty-page introduction by Masafumi Matsui of Kyoto University who, as well as providing interesting biographical notes on the Norwegian-born author, relates the scientific names used in the text to current nomenclature. Also supplementary to the original are portraits of the author, a map of the region and a superb lithograph by A. Saagmans Mulder of the Japanese giant salamander, *Andrias japonica*, taken from de Siebold's "Fauna Japonica".

Leonhard Hess Stejneger's own 600 pages provide accounts of 156 species, each of which features an illustration of the whole animal, a synonymy, a description of the type specimen and information concerning individual variation; where available, brief habitat and distribution details are given, together with lists of known specimens and localities. There are 35 plates, 409 text figures, keys, an index, a gazetteer of localities and an annotated bibliography.

It came as something of a surprise, to one reader at least, that this book should prove so readable. For a taxonomic work, written in his second language, Stejneger has on occasions employed a slightly informal style which gives the prose an unexpectedly contemporary feel. There is, in fact, rather little to complain about in this book. Poor printing obscures parts of some letters, without making them unintelligible, and there is a discrepancy between the number of pages claimed on the dust cover and the number actually present, but such minor flaws will certainly not deter anyone from buying one of the 800 copies printed.

Perhaps the reviewer may be allowed, in closing, to make a personal plea: is it not about time that someone produced a *new* English guide to the Japanese reptiles and amphibians?

Leigh Gillett
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Biology and Conservation of Sea Turtles (Revised Edition). Karen J. Bjorndal (Ed.). (1995). 615 pp., Smithsonian Institution Press, Washington and London. £23.25 (paper).

The first edition of this book was published in 1982, and reported the proceedings of a conference that took place in Washington DC three years earlier, in 1979. Despite the claim that this is a *revised* edition, most of the volume (569 pages to be precise) is exactly the same as in the 1982 edition, so reflects the state of sea turtle science about 17 years ago, not that of the early 1990s. Probably this is inevitable, since the original book consisted of a series of papers given at the conference by different authors; sensible modification would have been near-impossible.What is different is that a series of short updating chapters, brought together under a heading of '*Recent Advances in Sea Turtle Biology and Conservation, 1995*' has been added at the end of the book. Some of these chapters, while useful, are extremely perfunctory and do little more than direct the reader to recent literature sources; they are in no sense comprehensive literature reviews. The chimaeric structure of the volume means that a reader must constantly be aware that much of the material has been overtaken by increased scientific knowledge of turtle biology, new techniques (strikingly in the use of molecular methods of genetic/taxonomic investigation), further declines in turtle populations, and changing ideas of viable approaches to turtle conservation. Despite these criticisms, the book is still useful and its availability at an accessible price in paperback form is praiseworthy - the original hardcopy volume was relatively expensive.

The 1979 conference papers are grouped into three sections. The first of these, '*Sea Turtle Biology*', is introduced by that great turtle biologist, the late Archie Carr, who presented a contribution devoted to behavioural ecology. The section includes a seminal paper by Mrosovsky & Yntema on the temperature dependence of sex determination in sea turtles - this had great immediate implications for conservation practice in the 1980s and has since led to ideas concerning the impact of global warming, and even to possibilities of controlling sex in chickens! Other chapters (on tagging and population dynamics for instance) have been somewhat undermined by more recent evidence of very high rates of tag loss, and much better ideas of turtle longevity.

The second section, '*Status of Sea Turtle Populations*', is for me the most poignant of the book. It draws together population estimates from all parts of the globe, together with descriptions of conservation measures in place. Time after time, authors pointed out that populations were under pressure from fishing operations, beach development and unremitting egg collection. Seventeen years later, although in some places the line has been held, so often the authors must chorus 'we told you it would happen, you didn't listen!'. From a personal viewpoint I was drawn to the paper by Siow Kuan Tow and Edward Moll on the turtles of Malaysia. In 1979 they reported that sea turtles were already absent from the west coast of peninsular Malaysia, and that populations of green and leatherback turtles on the east coast had halved in the previous two decades. They described conservation methods that were either in place, or planned. I visited Terengganu in the mid-80s, and nesting leatherbacks numbers had fallen to hundreds, rather than the thousands that had nested in the early 1970s. Now, in the mid 1990s the populations are virtually extinct as predicted by Tow & Moll, destroyed by decades of exploitation and conflict with fishing operations, despite legislation that could, and should have saved them.

The third section, '*Conservation Theory, Techniques and Law*', is in many ways the most dated. Two chapters are concerned with the utility of turtle farming/ranching as conservation measures, one by a proponent, one by a detractor. The argument over turtle aquaculture rumbled through the 1980s, but is now dead, undermined by the long period between hatching and sexual maturity, by disease in overcrowded conditions, and by concerns that the market for turtle products would be stimulated, not diverted by such enterprises. Even the contention that they could be used to generate hatchlings or juveniles for release has been attacked by those concerned about genetic pollution. A chapter by Edward Klima and James McVey on headstarting the most vulnerable sea turtle of all, the Kemp's Ridley caught my attention. These scientists planned to establish a population of Kemp's ridleys in Texas, as a back-up for the single, vulnerable, natural breeding beach at Rancho Nuevo, Mexico. Their ambitious programme has since done much to establish the concept of 'living tags', young turtles in which portions of carapace and plastron are swapped to give permanently marked individuals. They also developed sophisticated 'superheadstarting' techniques, so that hatchlings were imprinted on the Texas beach. All of this was presaged in their brave 1979 paper, yet the headstarting programme has been abandoned (in 1993). In late 1996, the *Marine Turtle Newletter* reported that adult females, identified as living tags released in 1983-86 were finally coming ashore in Texas to lay their eggs. The section includes another landmark paper by Seidel & McVea, on the early development of turtle excluder devices (TEDs), to minimize the drowning of sea turtles in shrimp trawls. Although the shrimp fishery of the Gulf of Mexico and the SE states of the USA is still a major source of turtle mortality, TEDs have undoubtedly saved many sub-adult and adult animals.

Finally, there is the new added material . The editor admits that the contributors would each have preferred to write 30 pages rather than the three allotted. Would that she had compromised a little! Few of the 14 added 'chapters' are of self-contained value; exceptions include a perceptive essay on headstarting by Dr Jeanne Mortimer and a brief, depressing overview of the 1995 status of sea turtle populations by Colin Limpus.

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Okoboji Wetlands. A Lesson in Natural History. Lannoo, M. J. (1996). 156 pp. University of Iowa Press, Iowa City. $29.95 (cloth), $14.95 (paper).

This book is an unusual and eclectic presentation, describing the history and natural history of a wetland area in the Okoboji region of Iowa. The Okoboji Wetlands are an 11 000 year old system of temporary and permanent water bodies and marshland areas, originally created by glacial action. As long as European-originated colonizers have known the area it has been recognised as a place of natural beauty and biological richness.

The author's interest stems from his teaching and research work at Lakeside Laboratory, a field station of the State's three universities, originally founded by the alumni of the State University of Iowa. The book's self-proclaimed target readership is visitors to, and inhabitants of, the Okoboji region. The work consists of a series of historical documents which relate to the area, its wildlife, and to the field station; as well as contemporary accounts of the fauna of the region. These are woven together by commentary and analysis from Mike Lannoo, who, as an amphibian specialist, also contributes accounts of the amphibians of the region.

The historical accounts of Okoboji's fauna allow Lannoo to deduce that large mammals and some bird, fish and amphibian species have disappeared from the region. Lannoo justifies particular attention to the latter group, on the basis that amphibians are indicators of the health of wetlands. The wetland communities of Okoboji are primarily structured by the forces of drought and the periodic development of anoxic conditions, both of which tend to favour amphibian species rather than the fish which fare better in the deeper waters of lakes. Lannoo compares the current amphibian fauna (as surveyed in 1991/92) with the historical survey carried out by Frank Blanchard in 1920. This reveals that two species, the mudpuppy and the cricket frog, have disappeared from the area. Comparison of current status with accounts of the abundance of leopard frogs in the early 1900s from a 'frogger' (someone involved in the commercial capture and supply of frogs for human consumption) also make it clear that the abundance of surviving native amphibians has decreased.

Lannoo considers the factors that may have caused the eradication of the missing wetland species, which results, in part, in a critique of some fisheries practices. Human consumption itself may have caused initial depletions of leopard frogs, and drainage and pollution as a result of agriculture and human habitation may also share some blame. However, the introduction of game fish and bullfrogs to the wetlands, and the management practices instituted, including the application of the chemicals aquazine and rotenone, to favour fish productivity, have had deleterious consequences for the wetland ecosystem and its amphibian inhabitants.

Lannoo concludes by making recommendations for wetland management that should avoid the problems witnessed at Okoboji. The keystone of Lannoo's recommendation is an appreciation of wetlands as biological systems, valuable not only due to their biological productivity, but also in their actions as natural water treatment systems and in the limitation of flood damage. However, Lannoo warns that the functions of these systems can be disrupted by damaging their smaller components.

In meeting his own aim of raising awareness of, and generating pride in, local natural history, Mike Lannoo continues in the tradition of Lakeside Laboratory, envisaged by one of its founders, William MacBride, of 'bringing scientific work to the attention of people of every class and kind.' Consistent with this educational objective, is the fact that proceeds from the sale of Okoboji Wetlands will go to support Lakeside Laboratory's student scholarship programme.

John Baker
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EDITOR'S NOTE

The editor is grateful to the following for reviewing manuscripts submitted to the *Herpetological Journal*:

R. Alford, R. Altig, P. Arntzen, R. Avery, G. Baggott, J. Baker, R. Beattie, T. Beebee, P. Bishop, D. Blackburn, R. Blommers-Schlösser, K. Bonine, L. Brady, G. Brown, R. Brown, W. Brown, D. Bullock, D. Buth, J. Caldwell, J. Castanet, R. Cromie, R. van Damme, P. Daszak, J. Davenport, J. Diaz, K. Dodd, D. Dolmen, W. Dunson, M. Dyson, S. Eckert, S. Evans, J. Fa, L. Fitzgerald, A. Forsman, J. Foster, D. Frost, E. Gaffney, P. Galan, M. Garcia-Paris, A. Gardner, J. van Gelder, T. Gent, L. Gillett, G. Gollmann, G. Grigg, K. Grossenbacher, A. Hailey, M. Harvey, W. Heyer, W. Himstedt, M. Hoogmoed, R. Huey, H. Inns, P. Joly, J. Just, H. Kaiser, M. Kalezic, L. Kats, M. Klemens, S. Kuzmin, M. Lambert, L. Luiselli, A. Malhotra, J. Mateo, C. Miaud, A. Milner, C. McCarthy, R. McNeil Alexander, D. Nichols, G. Nilson, R. Nussbaum, D. Owens, V. Perez-Mellado, P. Pritchard, M. Ramirez Pinilla, C. Raxworthy, C. Reading, A. de Riqlès, Z. Rocek, J. Savage, M. van Sluys, A. Smart, G. Smith, J. Stamps, J. Stewart, D. Stiffler, H. Strijbosch, M. Swan, M. Thompson, R. Tinsley, D. Toews, M. Uchiyama, G. Ultsch, G. Underwood, M. Vences, B. Viertel, M. Veith, M. Wake, V. Wallach, M. Wilkinson, P. Withers, W. Wüster, J. van Wyk, G. Zug.

THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

(revised January 1992)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: full papers (no length limit); reviews and mini-reviews (generally solicited by a member of the editorial board); short notes; controversies, under 'Forum' (details available from the Editor); and book reviews. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance.

2. *Three* copies of all submissions, and illustrations, should be sent to the Editor. All papers will be subject to peer review by at least two referees

3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. Typesetting is greatly assisted if accepted manuscripts can be supplied on microcomputer diskettes. Authors are therefore strongly encouraged to produce manuscripts using a wordprocessor (preferably on a PC-compatible microcomputer).

4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of 5 words or less. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. Short notes (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.

5. The usual rules of zoological nomenclature apply.

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7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. Fig. 1. Colour photographs can only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.

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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. (1969*a*). 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. (1969*b*). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* **216**, 995–1002.

9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.

10. Proofs should be returned to the Editor by return of post. Alterations should be kept to the correction of errors; more extensive alterations will be charged to the author.

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