BREEDING BIOLOGY AND LARVAL DEVELOPMENT OF *LITORIA VERREAUXI* (ANURA: HYLIDAE)

*BY MARION ANSTIS***

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Introduction

Litoria verreauxi (Duméril), previously included in *Hyla ewingi* Duméril & Bibron (see Littlejohn 1963, 1965; Tyler 1971) is a hylid frog found along the coast of eastern Australia from Victoria to southern Queensland (Littlejohn 1965; Straughan 1966)†. Adult morphology in the Sydney area has been described by Copland (1957) as *H. ewingi verreauxi*, and by Moore (1961) as *H. ewingi*. Fletcher (1889) and Harrison (1922) provided some data on the breeding season, ova and larvae, while Moore (1961) briefly described advanced embryos and larvae. Martin (1965) described tadpoles from the Melbourne area but did not discuss embryonic development. Martin & Watson (1971) mention some life history characteristics. The present paper provides data on breeding biology and larval ecology and includes a detailed description of embryos and larvae.

L. verreauxi appears to be related to a complex of species including *L. ewingi*, *L. paraewingi*, *L. jervisiensis*, and possibly *L. burrowsi* (Martin & Littlejohn 1966; Martin 1967a; Watson, Loftus-Hills & Littlejohn 1971). Where data are available, comparisons are made with these taxa.

Material

Six egg masses of *L. verreauxi* laid in the laboratory, together with samples of larval material from the field, form the basis of the study. Egg masses came from an adult population, originally collected at Darke's Forest in 1970 and released in a garden at Penshurst. Frogs from adjacent areas in Penshurst may also have joined the population.

An egg mass from a pair of *L. ewingi* captured in amplexus at Lobethal, S. Aust. on 30.viii.1972, was maintained to hatching stages. Larvae of *L. paraewingi* from 2 km N of Glenburn, Vict. were examined for comparison. Collecting localities and dates are listed in Table 1.

Methods

A series of outdoor aquaria containing rainwater and vegetation was maintained at Penshurst and checked regularly for the presence of spawn. Three pairs (one in amplexus) were captured in the vicinity of the aquaria (two on 11.ix.1972 and one on 20.ii.1974) and placed in plastic bags containing water, twigs and vegetation. Oviposition behaviour of these three pairs was studied.

Embryos were maintained up to stage 25 in shallow water ranging from 14°–21°C. Larvae from the various localities were maintained separately in open outdoor aquaria, and individuals from some were reared to metamorphosis. The behaviour of larvae was studied both in aquaria and at field collecting sites. Food provided consisted of algae and other water plants, commercial fish food, boiled lettuce and occasionally meat. Water temperature during larval development ranged 8°–27°C. Specimens from each group were fixed at inter-

* 630 King George's Road, Penshurst, N.S.W. 2222.

† Straughan, I. R. (1966).—An analysis of species recognition and species isolation in certain Queensland frogs. Ph.D. thesis, University of Queensland (unpubl.).

TABLE 1

Breeding sites of Litoria verreauxi

Locality	Description of habitat	Collecting date	Stages	Other larvae present
Menai, 34°02′ S 151°01′ E	1. Permanent dam in dry sclerophyll bushland. Surface vegetation, rooted plants, mud substratum.	21.ii.1971	34–42	*Litoria aurea* *L. latopalmata* *Uperoleia marmorata* *Ranidella signifera*
	2. Concrete water vessel, permanent water, surface vegetation, mud substratum	16.ix.1972	34–41	
Penshurst, 33°58′ S 151°05′ E	Permanent outdoor aquaria in suburban garden. Surface and rooted plants	Numerous dates, 1970 to 1974	1–46	
Darke's Forest, 34°12′ S 151°58′ E	1. Permanent flowing stream, sandstone base, fast flowing sections, deep pools in dry sclerophyll bushland.	16.ix.1972	16–18	*Litoria jervisiensis*
	2. Permanent dams, little rooted and no surface vegetation, mud substratum	24.ix.1972 30. x.1972 2.xi.1972 6.xi.1972	26–40	*Limnodynastes peroni* *Litoria peroni* *Ranidella signifera*
Ourimbah, 33°22′ S 151°22′ E	Semi-permanent, small, slowly flowing creek, shallow pools, rooted vegetation, mud substratum. Cleared farmland in wet sclerophyll forest	19.ix.1973	25–33	*Ranidella signifera*
Glen Alice, 33°02′ S 151°12′ E	Semi-permanent, shallow pond, grass bottom, in open cleared farmland with surrounding woodland	1.vi.1974	25–28	*Limnodynastes tasmaniensis*
Spring Creek, 30°29′ S 152°24′ E	Permanent creek, slowly flowing small pools, sandy and basalt substratum. Wet sclerophyll forest, partly cleared	25.i.1973 25.xii.1973 18.iv.1973	30–46 25–42	*Mixophyes balbus* *Ranidella signifera* *Litoria glandulosa* *L. pearsoni*
Dorrigo, 30°20′ S 152°43′ E	Small, slowly flowing creek, surface vegetation, mud substratum. Cleared rainforest farmland	26.xii.1974	28–43	*Mixophyes fasciolatus* *Adelotus brevis*
Rouse Hill, 33°42′ S 150°55′ E	Permanent waterhole in cleared paddock. Dry sclerophyll bushland area, farmland	19.xii.1972	27–42	*Litoria caerulea* *Ranidella signifera*

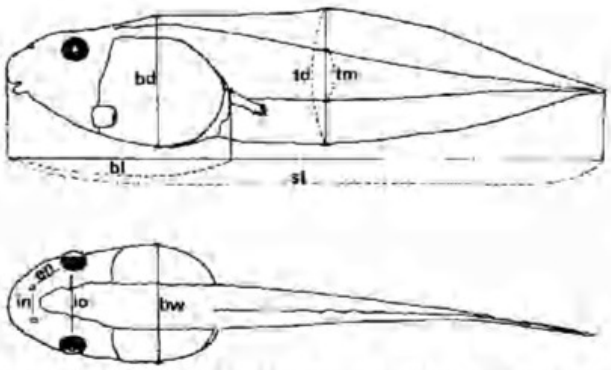

Fig. 1. Lateral and dorsal views of larva showing measurements for morphometric characters.

vals in 4% formalin, after being relaxed in 1% chlorbutol solution; larger specimens were injected with a small quantity of formalin before final fixation.

Measurements were taken with vernier callipers reading to 0.1 mm or an ocular micrometer (reading to 0.01 mm). Drawings were made using a drawing tube attached to a stereoscopic microscope. All measurements and drawings are based on preserved specimens, while descriptions are of both preserved and live material. The staging system used is that of Gosner (1960). Abbreviations and definitions of larval morphometric characters (Fig. 1) are: ST—total length (tip of snout to tip of tail); BL—body length (tip of snout to junction of body wall and tail musculature); BW—maximum body width; BD—maximum body depth; TD—maximum tail depth; TM—depth of tail musculature (measured in line with TD); IO—inter-orbital span (minimum distance between the eyes, measured at the central inner edge of each eye); IN—internarial span

(minimum distance from eye to naris); EN—distance from eye to naris; MW—maximum width of oral disc.

Results

Calling activity: The mating call has been described by Littlejohn (1965). Males at Penshurst call throughout the year, with the most intense activity on mild, wet nights during spring and summer. Diurnal calling mostly occurs during and after rain. Males call while afloat near the edge of ponds by night, or from low vegetation or ground near the water by night or day. At 2300 hrs on 20.ii.1974 at Penshurst, during light rain, a silent male surfaced in an aquarium about 4 cm from a calling male. The latter turned to face the former and, after a brief pause, swam slowly towards him, calling in softer, separate notes (quite distinct from the mating call) and attempted amplexus. The silent male immediately swam off. The calling male did not follow, but resumed a normal mating call.

A similar behavioural sequence preceded amplexus in one of the pairs captured on 11.ix.1972, the male emitting soft, separate notes as he approached the female.

Oviposition: Oviposition at Penshurst has been observed in February, March, June and September–December. The following description is a composite of observations of the three pairs studied.

When frogs were collected on 11.x.1972, air temperatures 2 cm above water were 18°–19°C and surface water temperatures 19°–23°C. Amplexus commenced in these pairs at 2000 and 2325 hrs. Eggs were laid in separate batches attached to twigs or reeds over a period of hours (Table 2). Before oviposition, the female showed lateral abdominal contractions, either simultaneously or alternately. These contractions usually became more powerful as oviposition was near and lasted about one second, with two or more occurring in succession.

In a typical behavioural sequence, a pair submerged and the female grasped a twig with one hand. She dorsiflexed her body with the hind limbs extended and, as the batch emerged, the male lowered his vent towards the eggs and cupped his feet around, so holding them (Fig. 2a). The sides of the male then undulated and his feet moved up and down in a brief fanning motion over the eggs. This process of oviposition and fertilisation lasted 3 sec. The female ventriflexed, drawing her legs back under her body, and the male rolled the batch down to her feet (Fig. 2b). The female held the batch motionless for 40 sec. She then pulled herself around the twig in spiral fashion, wrapping the eggs round it with her feet. The pair left the eggs and returned to the surface. After 1.5–7.5 min. the entire process was repeated, and 5 min.–2 hr elapsed before further batches were laid.

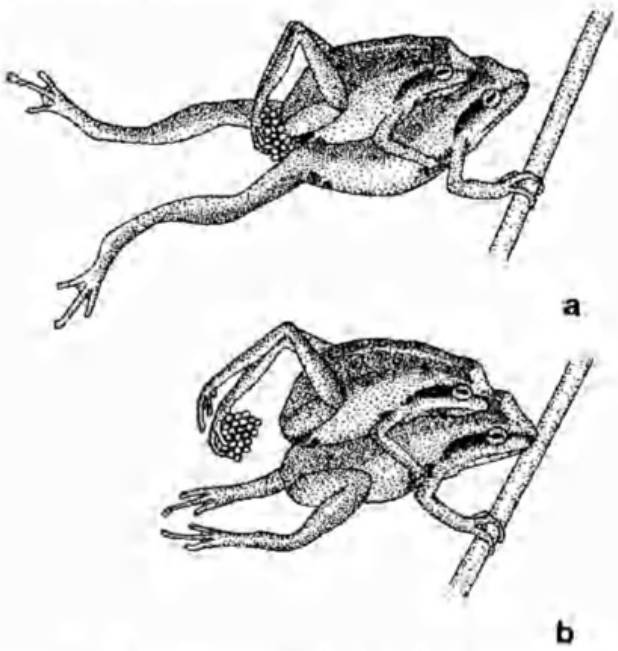

Fig. 2a. Oviposition with the male receiving and fertilising the eggs.
Fig. 2b. The male pushes the batch down to the female's feet.

Variations were: (1) Nearing the end of amplexus, two or three batches were laid in very close succession, each being held by the feet of the female for 40–60 sec. before the ensuing one was laid. The resulting composite batch was then attached to supporting material. (2) Females varied in their attempts to spread

TABLE 2
Oviposition behaviour

Pair	Total duration of Amplexus	Duration of egg-laying period	Duration of single batch oviposition	Batch holding time (female)	n	Total eggs laid
1	5 hr 15 min.	2 hr 18 min.	2–4 sec.	35–60 sec.	15	757
2	Unknown	3 hr 47 min.	2–4 sec.	35–60 sec.	23 or 24	1,011

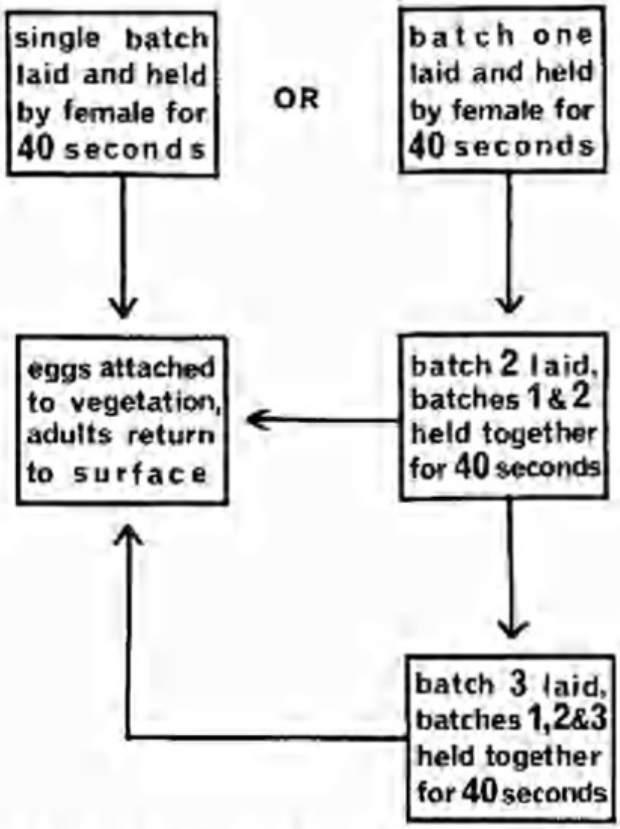

Fig. 3. Oviposition cycles during which a single batch is laid and attached to vegetation, or two or three are laid in close succession before attachment.

out the eggs in spiral fashion, sometimes swivelling around the twig only once or not at all, resulting in thicker clumps of eggs. (3) One female used her left hand to grasp and pull free some eggs which had adhered to her venter, before attaching the batch to vegetation.

Females had more difficulty in wrapping a composite batch around a twig, and often abandoned the eggs as a thick mass. In aquaria lacking vegetation or twigs, egg masses have been found in thick clumps on the substratum, in water up to 50 cm deep.

The final stages of amplexus in one pair were: at 0100 hrs the female made movements similar to the croaking motions of males, but produced no sound. At 0108 hrs she submerged and both male and female began typical ovipositional behaviour, but the female remained in the dorsiflexed position for 7.7 sec. (4.7 sec. longer than average) and produced no eggs. Two sec. later the pair fell apart, both floating motionless on their sides just under the surface, with limbs tightly adpressed against the body. After 10 sec., the male

Fig. 4. Two batches of eggs joined and attached to a stem. Filamentous algae are entwined amongst the egg mass.

recovered from this state of suspension and surfaced, the female doing so 5 sec later. A second pair behaved similarly, except that the period of motionless suspension was shorter. The basic cycle of oviposition behaviour is shown in Fig. 3. Laying of all eggs comprises a number of such cycles.

Ova: In natural environments egg masses are attached to submerged reeds, twigs or grasses usually close to the surface (Littlejohn 1963). The eggs cohere and the inner ones stick to the supporting material. There is a single layer of jelly around each egg, but within a mass the individual capsules merge and are not clearly defined (Fig. 4).

The mean diameters of eggs and capsules in stages 1 and 8 are shown in Table 3. Ova generally have a dark brown animal pole and an off-white, yellow or orange vegetal pole. All ova from a single female are the same colour. The animal pole gradually lightens from gastrulation onwards.

The number of eggs in 20 single batches ranged from 1–52 (mean 30). Three "double" batches contained 64, 78 and 79. The total complements of four females were 1,011, 757, 632 and 522.

Development of embryos: After fertilisation there is no distinct grey crescent. Cell division appears normal, although not as symmetrical as in Gosner's (1960) diagrams. The vegetal pole always divides later than the animal pole. At stage 17 (tail bud: Fig. 5a), the head region is well defined, showing optic bulges, gill plates, U-shaped adhesive organ and a slight stomodaeal pit. The posterior crescent of the adhesive organ is less distinct. In some embryos

the visceral arches and a slight pronephric bulge are discernable. The tail bud is straight and points dorsally, with no obvious tail fin rudiment. In late stage 17, just before muscular movement begins, the tail bud extends and points either to the right or to the left, and the posterior crescent of the adhesive organ almost disappears, yielding two separate organs which are heavily pigmented. Embryos in stages 17 to 20 have a yellow yolk sac and are light brown elsewhere.

The embryos begin hatching when they have reached stages 19 and 20. At stage 20 (Fig. 5b) the gills are small, just functional and non-pigmented. The optic bulges are more defined, and there is a small crescent of melanophores around the anterior edge of each. The stomodaeal pit has deepened and the adhesive organs are prominent. The yolk sac has elongated and is generally narrow, and there are small areas of pigment along its dorsal edge, and between the optic bulge and olfactory pit. The area above the olfactory pit is clearing and the tail fins are a translucent milky white.

With the temperature regime prevailing during early development, hatching was complete after 147 hr when most embryos were in stages 21–23. The external gills are fully developed in stage 21 (Fig. 5c). The tail fins and cornea clear during stage 22; the operculum partly covers the gills, and the distribution of melanophores increases over the yolk sac, beneath the eyes, around the nares and along the dorsal surface of the tail musculature. At stage 23 the gills are reduced, the external nares are open, the stomodaeal pit deepens further and the oesophagus begins to differentiate. The anal tube is developing and the fins, now transparent, take on their characteristic arched shape. Generally, pigmentation increases, dispersing into the pattern typical of the larva. The yolk sac is pale yellow beneath the layer of melanophores, while other dorsal and lateral areas surrounding the pigment, become transparent. However one group of embryos at this stage lacked dark pigment (except for the eyes), and appeared yellow. These embryos did not develop melanophores until stage 25.

At stage 24 the mouth-parts have developed oral ridges and a small non-keratinised beak, the oral suckers have diminished, and the operculum closes on the right side. The anal tube is partly open in some embryos. During stage 25 the formation of mouthparts is virtually completed, the beak becoming keratinised and

TABLE 3

Dimensions in mm of embryos and larvae of L. verreauxi *from Penshurst* (means, with ranges in brackets)

Embryos

Stage	n	Embryo diam.	Capsule diam.
1	10	1.23 (1.19–1.23)	4.31 (3.53–4.92)
8	8	1.20 (1.15–1.23)	4.55 (4.26–4.92)
9 & 10	9	1.28 (1.23–1.39)	3.88 (3.44–4.35)
14	9	1.55 (1.48–1.64)	4.28 (3.74–4.92)
15	9	1.74 (1.68–1.80)	4.41 (4.10–4.92)
17	10	2.11 (1.85–2.30)	4.39 (3.61–6.40)

Stage	n	Embryo diam.
20	10	5.83 (5.62–5.99)
21	10	6.27 (6.07–6.44)
22	10	6.40 (6.15–6.64)
23	10	6.98 (6.23–7.30)
24	9	7.26 (6.72–7.71)
25	10	8.45 (7.87–9.18)

Larvae

Stage	n	Body length	Total length
26	10	10.16 (9.02–12.79)	23.6 (19.0–31.4)
27	10	11.11 (10.50–11.64)	24.2 (21.2–27.2)
28	10	10.85 (9.68–11.91)	24.0 (21.0–27.6)
29	9	11.16 (10.33–11.97)	24.5 (24.6–27.2)
30	10	12.88 (11.15–13.78)	29.1 (25.2–31.5)
31	10	13.65 (12.30–15.42)	33.6 (27.5–39.4)
32	7	13.40 (11.91–14.27)	30.5 (27.0–33.2)
33	8	14.31 (13.94–15.58)	32.6 (31.0–34.0)
34	8	14.85 (13.12–15.74)	34.7 (30.1–37.6)
35	10	16.65 (14.76–19.68)	41.1 (33.0–48.8)
36	10	16.15 (15.35–18.61)	41.4 (34.8–47.2)
37	8	16.22 (14.92–17.22)	39.5 (36.4–44.8)

Stage	n	Body length	Total length
38	6	16.84 (15.00–18.00)	43.2 (39.6–46.0)
39	6	17.27 (16.73–18.32)	45.6 (42.0–51.9)
40	10	16.87 (14.76–18.37)	46.6 (39.2–52.2)
41	10	17.09 (16.56–18.20)	48.2 (45.0–52.9)
42	3	16.13 (14.27–17.38)	43.1 (40.5–45.1)
43	4	14.51 (14.27–14.92)	38.6 (37.4–39.7)
45	10	16.3 (14.9–18.6)	—
46	18	15.3 (13.2–17.3)	—

labial teeth developing on the oral ridges. The labial papillae may not reach their total number until stage 26 or later. The spiracle becomes functional and the anal tube is fully open. The remnant adhesive organs gradually disappear during this stage.

Measurements of embryos are shown in Table 3.

Larvae: A composite description of 10 larvae at stage 35 (Figs 5d–f) from Penshurst follows: Body widest across the mid region of the abdomen and ovoid. Snout evenly rounded in dorsal view and tapers to a truncate edge in lateral view. Nares dorsal and raised on very short tubes which open antero-laterally. Eyes lateral and relatively large. Spiracle sinistral, ventrolateral and not visible from above. It opens in a porstero-dorsal direction and diameter of the spiracular tube decreases slightly from its origin to its opening. Anal tube dextral, very short, of small diameter and opens about halfway up the ventral fin. Tail fins arched and taper to a fine point. Dorsal fin extends midway up the body, deepest approximately halfway along its length. Ventral fin deepest along its anterior third. Tail musculature moderately thick, narrowing to a fine point posteriorly.

Mouth antero-ventral in position and has border of papillae around all but the anterior margin (Fig. 6). In some specimens there is also a median gap along the posterior margin (possibly caused by damage). Papillae most numerous laterally. Two upper and three lower rows of labial teeth, two upper being of approximately equal length in most specimens. First two rows in the lower labium are also about equal, third lower row is usually the

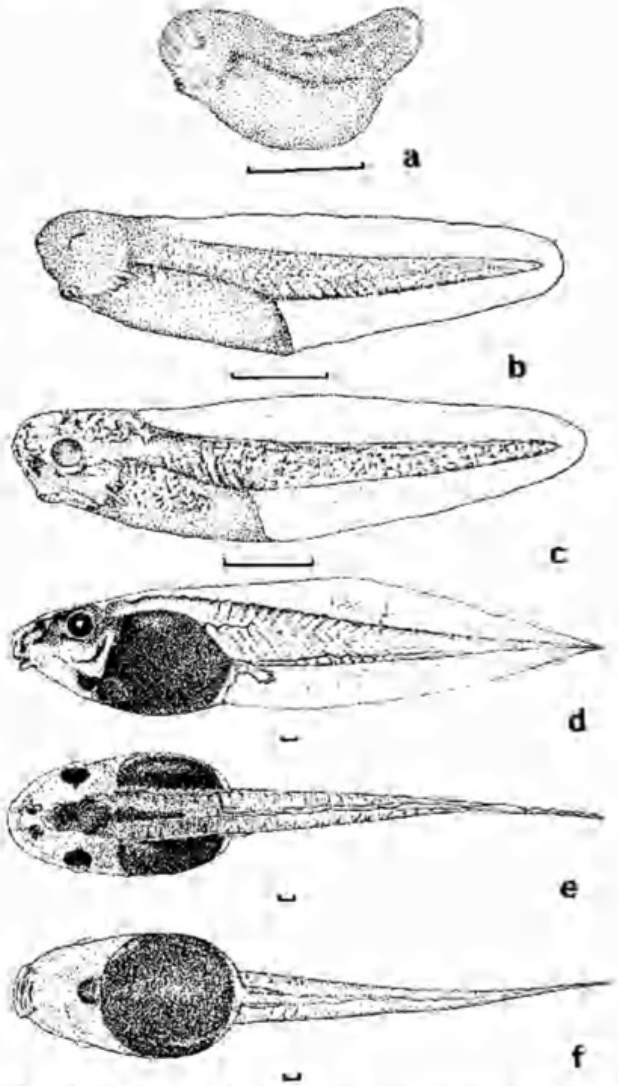

Fig. 5. Embryological and larval development of *Litoria verreauxi*, Penshurst. (Bar represents 1 mm). Stages: a—17, b—20, c—21, d—36, e—36, f—36.

shortest. In some specimens a partial median gap occurs in second lower row and other rows may be interrupted at various points, probably through damage. Beaks of moderate proportions, serrations fine on inner edge of lower beak and very fine on the upper beak.

The only consistent geographic variation noted was in specimens from Spring Creek, most of which had more massive beaks and two pigmented areas below the lower beak (Fig. 6b). Specimens from Dorrigo also showed a tendency towards more massive beaks. It was noted that specimens from the northern localities generally had shallower fins than most southern specimens (Table 4). Body dimensions of larvae are given in Table 3.

In life the dorsal surface varies amongst individuals from light golden to a very dark

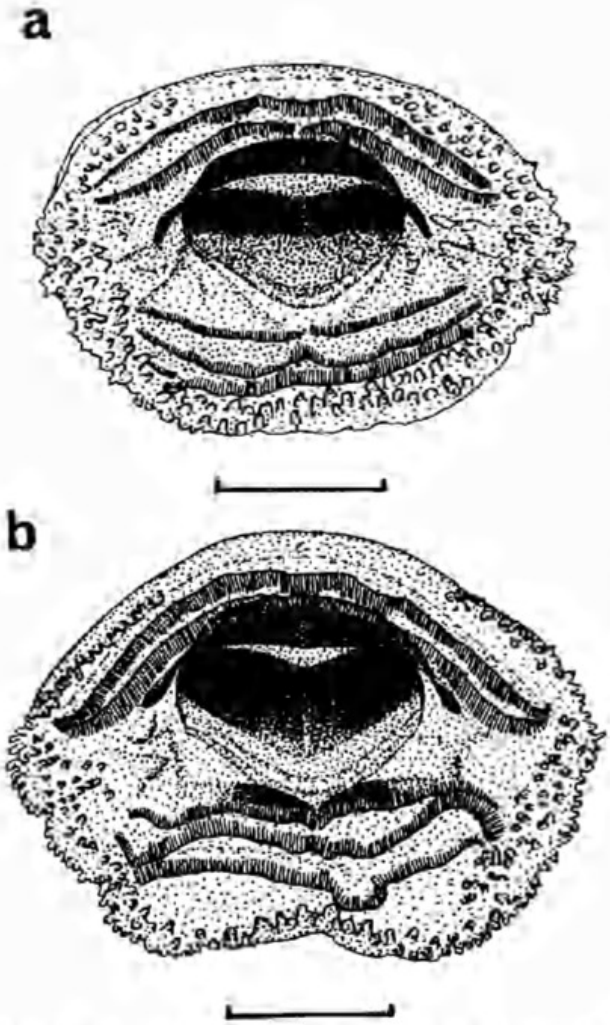

Fig. 6. Mouthparts of *L. verreauxi*. a, from the southern site of Penshurst; b, from the northern site of Spring Creek (bar represents 1 mm).

brown (almost black). In some specimens the pigment is mottled. The areas of skin over the trabeculae cornua, central nervous system (brain and spinal cord to base of tail), the abdomen and surrounding the nares, are darker. There is a copper-gold sheen ventrally and laterally over the abdomen. In lateral view the areas covering the pharynx and buccal cavity (excluding eyes) are transparent (except for some melanophores between the eye and naris), and the gills, heart and developing forelimbs are visible. From the ventral aspect the areas over the gills, heart and buccal cavity are unpigmented.

The tail musculature is cream with irregular dark blotches over the dorsal surface, and partly over the lateral surface. In generally darker larvae the musculature may be uniformly pigmented. The dorsal and ventral fins

TABLE 4

Proportions in mm of L. verreauxi *larvae from different localities*

(means, with ranges in brackets)

	Northern (Spring Creek, Dorrigo)	Southern (Penshurst)
Stage	35 & 36	35 & 36
n	7	10
ST	35.1 (30.9–41.2)	43.1 (36.3–48.8)
BL	13.69 (12.46–16.56)	17.27 (15.58–19.68)
BW	7.74 (6.72–8.86)	10.26 (8.69–11.48)
BD	7.79 (6.56–9.33)	10.50 (8.86–12.14)
ID	7.98 (6.48–9.68)	10.19 (8.53–12.30)
IM	2.68 (2.13–3.28)	3.60 (2.79–4.59)
IO	3.92 (3.44–4.55)	5.53 (4.66–6.40)
IN	2.01 (1.72–2.21)	2.64 (2.46–2.95)
EN	2.25 (2.13–2.69)	2.69 (2.38–3.12)
MW	2.03 (2.95–4.43)	4.10 (3.61–4.66)

vary from dusky (in dark larvae) to almost transparent (lighter larvae), with parts of the tail vascular system pigmented. Larvae with mottled pigmentation over the body also have mottled tails. The iris is golden.

Specimens which were dark in life may retain much of this pigment in preservative. Those which were light golden become an off-white colour in all but the darker areas, and the skin is clearer than in life. The copper-gold sheen is lost and the abdomen may appear dark shiny blue for some time in preservative, then eventually turn black. The iris loses its golden colour and also appears black.

Larval behaviour: After hatching the embryos remain close to the egg capsules until about stage 24. During stages 25 to about 27, the larvae are most often found in the shallow areas of ponds, particularly near the edge, but beyond this stage a much greater water space is utilized.

The larvae are of the active, nektonic type (Orton 1953) and spend much of their time hovering in the water by rapidly oscillating the tail tip (flagellum). They frequently cruise slowly to the surface with head uppermost at about a 45° angle, using only the flagellum for propulsion. When feeding at the surface, they

often position themselves almost vertically and can remain suspended at this, or any level in the water. They are capable of sudden spurts of speed (during which they may use the entire tail and body), and rapid changes of direction (making use of the deep fins), when disturbed. As well as feeding at the surface, the larvae graze on vegetation and other material in any zone of the pond and scavenge in bottom sediments. The variation in larval pigmentation appears to be related to characteristics of the habitat. Specimens in muddy water, or clear water over a dark substratum, usually range from dusky brown to almost black, while those in clear water over a light substratum tend to be golden, with the darker areas contrasting, but less pronounced.

Larval life span and metamorphosis: Metamorphosis of larvae reared from eggs laid at Penshurst on 11.ix.1972 began on 10.xii.1972, giving a spring-summer larval life span of 90 days. Metamorphosis of larvae from egg masses laid on 23.x.1971 occurred from late December to early March. Metamorphosis was also recorded at Penshurst in September 1972 and at Menai from 27–29.ix.1972. It is therefore known to occur from September–March, but probably takes place at other times because egg masses have been found in most months of the year.

The body lengths of 10 juveniles at stage 45, and 18 at stage 46 are shown in Table 3. At these stages the juveniles closely resemble the adults in colour, but lack the deep orange on the anterior and posterior surfaces of the thigh, and the black spots in the groin. Pale orange thigh colouration is visible in some juveniles at stage 46.

Discussion

Calling activity: Fletcher (1889) and Harrison (1922) noted that calling occurs throughout the year, and Moore (1961) observed calling activity from the end of July 1952 to late April 1953. Watson *et al.* (1971) record calling activity in all months except July and found that *L. verreauxi* males when sympatric with *L. ewingi* usually call on land up to 25 m from water, and only rarely in water. This latter behaviour contrasts with that of males at Penshurst and Darke's Forest which commonly call in water.

A call distinct from the mating call, given by the male on approaching a potential rival or mate, has been observed; its function is not known. More observations are necessary to establish the extent of behavioural variation in this species. A similar call has been observed in *L. ewingi* (Anstis 1976).

Oviposition: Harrison (1922) found spawn in Sydney every month of the year, and Moore (1961) collected embryos in August, 1952 at Killara. Fletcher (1889) found a pair in amplexus in June, 1885 and stated that the species "probably breeds nearly throughout the year". This agrees with the oviposition dates recorded at Penshurst.

Oviposition has been observed in few Australian hylids. Watson *et al.* (1971) described part of the behaviour associated with egg-laying in *Litoria paraewingi*, and I have observed oviposition in *L. citropa*, *L. dentata*, *L. freycineti* and *L. glauerti*. Some of the ovipositional patterns in *L. verreauxi* are unique, notably the action of the male pushing the clutch down to the feet of the female where the eggs are held motionless for a short period.

The behaviour of the male in cupping his feet around the batch and rapidly "fanning" the eggs may serve to distribute the seminal fluid around the eggs within a more confined space and thus aid fertilisation. A similar although somewhat briefer process occurs in the ovipositional behaviour of *L. citropa*, *L. dentata* and *L. glauerti* (Anstis unpubl.). By holding the batch still for a period of some seconds, the female may also aid fertilisation in allowing time for sperm penetration before the eggs are attached to supporting material.

It is not known whether the abdominal contractions in the female prior to egg-laying were the sole factor in extruding the eggs, or whether the pressure exerted by the clasp of the male aided the process.

The attachment of eggs to vegetation in a spiral movement has been recorded by Harrison (1922) for *L. verreauxi* (as *H. ewingi*) and by Watson *et al.* (1971) for *L. paraewingi*. Harrison's statement that the female moved "right around the stalk at the moment of laying" is not borne out by the present study, but it is possible that Harrison did not see the entire egg-laying procedure. Watson *et al.* (1971) state that a female of *L. paraewingi* observed in the field "held onto a submerged grass stem, and pressed the cloaca to the stem as the eggs were extruded; then the pair pivoted around the stem while attaching the eggs". Such behaviour would appear to be similar to that of *L. verreauxi* except that in the latter, the female holds the eggs still before

attachment and was not observed pressing the cloaca to the stem during egg extrusion. In the three oviposition sequences observed in this species, the extent to which batches of eggs were spread around the supporting vegetation varied. Observations have indicated that the mortality rate of embryos is lower in smaller well-spread batches attached to a stem. Larger masses of eggs on the bottom of aquaria without vegetation suffer high mortality from about stage 9 onwards, possibly due to inadequate oxygenation resulting from the thickness of the egg mass and the depth of the water where they lay. The attachment of two or three batches together as one also tends to increase mortality. After death of an embryo, a fungus develops over the egg capsule.

The manner of termination of amplexus varies amongst hylids, but often the last ovipositional sequence is longer than any other and is followed by separation either immediately or a few seconds later, e.g. in *Hyla versicolor* (Fouquette & Littlejohn 1960), and *Litoria dentata*, *L. glauerti* and *L. citropa* (Anstis unpubl.). *L. verreauxi* also follows this pattern; however, the brief period of total immobility of both male and female after separation has not been recorded in other species.

Ova: The significance of eggs being deposited in small batches has been discussed by Pyburn (1963) and Martin & Littlejohn (1966). Harrison's (1922) observation that the eggs are "attached in a cylindrical mass numbering upwards of a hundred eggs to grass stalks and similar submerged objects" is probably based on cases where two or three batches were attached as one.

The ovidiameter in stages 1–8 (1.21 mm) is in agreement with Harrison's figure of 1.2 mm. The ovidiameter of *L. ewingi* has been recorded as 1.65 mm (Martin & Littlejohn 1966) and that of *L. ewingi* and *L. verreauxi* as 1.7 mm (Martin, Littlejohn & Rawlinson 1966). A series of eggs of *L. ewingi* laid in Adelaide during September 1972, have mean diameters of 1.18 mm (at stage 1), 1.20 mm (stage 5) and 1.68 (stages 12–13); measurements similar to embryos of *L. verreauxi* at the same stages (Table 3). It would seem likely therefore that measurements by Martin *et al.* may have been taken from embryos at about stages 11–13.

The eggs of *L. paraewingi* are similar to those of *L. ewingi* (Watson *et al.* 1971). Those of *L. jervisiensis* can readily be distinguished from other members of the complex by the larger ovidiameter (2.33 at stage 10: Martin & Littlejohn 1966). Eggs of *L. burrowsi* can be distinguished from those of the *L. ewingi* group by the presence of two jelly layers around the ovum. The ovidiameter of this species at stage 14 is close to that of *L. jervisiensis* at the same stage.

Embryos and larvae: The larvae of the *L. ewingi* complex are of the common hylid type (Martin 1967b) as is *L. burrowsi*. The drawings by Martin (1967a) of *L. burrowsi* larvae show a tail not as finely pointed and fins not as deep as in members of the *L. ewingi* complex. The body shape also appears somewhat different. *L. paraewingi* larvae are similar to those of *L. ewingi* "except that the tail fins (especially the dorsal fin) . . . are more heavily pigmented" (Watson *et al.* 1971). Specimens of this species examined are more uniformly pigmented than *L. verreauxi*, and three specimens at stage 26 (mean total length 12.9 mm; body length 7.02 mm) are much smaller than *L. verreauxi* at the same stage. Such size differences may be related to environmental factors.

The mouthparts of the group are basically similar, having a formula of

$$\frac{1 \quad\quad 1}{1 \quad\quad 1}$$
$$2$$

All have a median gap in the papillae on the upper lip, the extent of which varies amongst individuals of the same species. The number and size of the papillae is variable between species; those of *L. jervisiensis* are more numerous and tightly grouped than in *L. verreauxi*, while those of *L. paraewingi* are a little larger and less numerous. The larvae of *L. jervisiensis* possess larger, darker and more massive beaks than *L. verreauxi* and in a number of specimens of the former species from Darke's Forest, the central edge of the upper beak curves slightly below the level of the rest of the edge, unlike *L. verreauxi*. The two pigmented areas below the lower beak in *L. verreauxi* from Spring Creek, are not found in other members of the *L. ewingi* complex.

Larval behaviour and adaptation: All the larvae of the *L. ewingi* group are nektonic and generally exhibit behaviour patterns similar to those described for *L. verreauxi*. However, differences occur in the larvae of *L. jervisiensis* which have been observed schooling together in groups of 20 or more in the mid-level of the water. Individuals from the group move at

different times to the surface where they may take air (Anstis, unpubl.). Larvae of *L. verreauxi* were never observed congregating in this manner.

Larval life span and metamorphosis: Data on larval life span are mainly limited to specimens in captive conditions. Moore (1961) records a laboratory life span of three months for *L. verreauxi* which agrees with one of the groups raised at Penshurst. Harrison (1922) found that larvae in aqnaria "required upwards of three months" to reach metamorphosis, but believed seven to eight weeks to be normal life span in the field during summer. This is considerably less than the approximate minimum of 79 days for one group in the present study, but this difference may simply reflect different culture and temperature conditions. Further observations are necessary to ascertain the average life span of this species in the field.

Moore (1961) records the body lengths of 11 newly metamorphosed *L. verreauxi* as 14.3–17.00 mm: consistent with measurements of specimens in the present study (Table 3). Martin (1965) gives a range 11.1–13.6 mm for newly metamorphosed *L. ewingi*, which are generally smaller than *L. verreauxi*, and Martin & Littlejohn (1966) 15.6–19.7 mm for *L. jervisiensis*. No data on *L. burrowsi* and *L. paraewingi* are available.

The overall life cycle of *L. verreauxi* appears quite similar to that of other members of the *L. ewingi* complex in the adaptations to still water situations, although *L. jervisiensis* differs noticeably in the details of its life history (Martin & Littlejohn 1966). More data are necessary before useful comparisons can be made between the life histories of *L. burrowsi* and the *L. ewingi* complex.

Acknowledgments

I gratefully acknowledge the receipt of a research grant from the C.S.I.R.O. Science & Industry Endowment Fund, which has greatly facilitated this study. Dr Harold Cogger, Mr Harry Ehmann, Dr Norman Gradwell, Dr Angus Martin and Mr Michael Tyler read and constructively criticised the manuscript. Thanks are also due to Mr and Mrs D. Anstis for assistance in various ways.

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