just above high-tide mark to approximately 70 cm below (Alexander & Ewer 1969). They are usually associated with *Spartina, Triglochin, Juncus* or *Sarcocornia* beds. The crabs are easily frightened by sudden movement, but soon reappear to sit in the mouths of their burrows or walk around when conditions return to normal.

According to Alexander & Ewer (1969), two types of burrow are inhabited by *S. catenata.* The first is formed on mudflats and consists of a more or less vertical shaft extending downwards for 15–20 cm. The shaft which may have inclined side entrances, leads into a nest containing free water. It can be inhabited by up to six crabs. The second type of burrow is found in vertical erosion scarps or 'salting cliffs'. Such burrows consist of openings leading into a network of inter-connecting tunnels which may reach back 40–50 cm from the scarp face and contain free water at the lower levels (Alexander & Ewer 1969).

In Table 1 the surface features of the burrows described above have been summarized to assist in rapid identification.

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Natalobatrachus bonebergi (Anura: Ranidae): aspects of early development and adult size

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The early development and adult size of *Natalobatrachus bonebergi* were investigated. Newly hatched tadpoles were normally about 12,5 mm long. Fore-limb emergence occurred at a total length of 35 to 41 mm after 60 to 125 days of development in the laboratory. Body length was 12 to 13 mm at the end of metamorphosis, and reached two to three times this length at sexual maturity. Hind-limb growth corresponded closely in natural and laboratory populations and served to indicate pre- and pro-metamorphic phases. Rapid increase in hind-limb length occurred only after tadpoles had reached 30 mm in total length.

Die vroeë ontwikkeling en volwasse grootte van *Natalobatrachus bonebergi* is ondersoek. Pas uitgebroeide larwes was normaalweg nagenoeg 12,5 mm lank. Voorste ledemaatdeurbraak het plaasgevind by 'n totale lengte van 35 tot 41 mm na 60 tot 125 dae laboratoriumontwikkeling. Aan die einde van metamorfose was liggaamslengte 12 tot 13 mm, terwyl geslagsryp indiwidue twee tot drie keer hierdie lengte bereik het. Groei van die agterste ledemaat was eenders in natuurlike en laboratoriumbevolkings en kon dien om pre- en prometamorfose-fases aan te dui. Vinnige toename in agterste ledemaatlengte het eers voorgekom nadat die larwes 'n lengte van 30 mm bereik het.

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Natalobatrachus bonebergi Hewitt & Methuen, 1913, has a limited coastal distribution in central and southern Natal and north-eastern Cape Province (Poynton 1964). Egg masses are suspended above water on various types of substrate, mostly plants. On hatching, tadpoles drop into the water to complete their development.

Wager (1931, 1952) described hatching and larval development in *N. bonebergi,* but was unsuccessful in rearing tadpoles under laboratory conditions. He was consequently unable to relate developmental changes to tadpole age. The only other accounts of *N. bonebergi* larval morphology and identification are those of van Dijk (1966) and Wager (1986). Van Dijk (1972) referred to the rheophilic, bottom-dwelling habits of the tadpoles and pointed out the lack of information on natural habitat preferences and development.

The present study supplements existing knowledge on *N. bonebergi* early development and hatching, larval development up to metamorphosis and adult size range. Studies were carried out mainly under laboratory conditions but were supplemented with data obtained from natural populations. Data on adult size ratios were obtained exclusively from samples of natural populations.

Intact egg masses of *N. bonebergi* were collected in the Vernon Crookes Nature Reserve (30°16′S / 30°37′E). Egg masses were kept suspended over water at 23°C (± 1,5°C) and approximately 80% relative humidity until hatching was completed.

Hatched tadpoles were collected daily and reared at densities of no more than four individuals per litre of dechlorinated tap water. They were fed on a suspension of dried pulverized lucerne and goldfish flakes. At the onset of metamorphosis, they were transferred to shallow water. Post-metamorphic frogs were fed on small termites, cockroaches and flies.

Adult frogs were caught at night in vegetation overhanging slow-flowing, shallow streams in the indigenous, coastal forests of the Vernon Crookes Nature Reserve.

Tadpoles were anaesthetized with 0,02% MS 222 (Sandoz) before measurement.

Egg membranes and hatching

Eggs adhered to one another in the egg mass, but were easily pried apart. The developing embryo was surrounded by inner and outer membranes. In the early stages of development, up to gastrulation, the embryo was 2,5–2,8 mm in diameter and the external diameter of the egg 4 mm. The outer membrane was about 1 mm thick, gelatinous and adhesive. As lengthening of the embryo proceeded, the external diameter of the egg increased and reached 8–9 mm at onset of hatching. The egg became flaccid and hatching occurred when the membranes broke and the tadpole dropped into the water.

Size at hatching and the stage of development reached, varied in different egg masses. Two individuals from one egg mass both measured 12 mm, 10 from another had a mean of 9,6 mm (*S.E.* 0,2) and 14 from a third had a mean of 12,6 mm (*S.E.* 0,2). The batch of tadpoles which had a mean of 9,6 mm at hatching, had hatched at an early developmental stage, approximately Gossner's stage 20 (*cf.* Duellman & Trueb 1986) but without external gills. In contrast, the 12,6-mm tadpoles hatched at approximately Gossner's stage 24. They showed a more advanced development with internal gills and mouth functional, and keratodonts and circumoral papillae present.

Larval growth and metamorphosis

The rate of larval growth was variable. In two samples of larvae, representing extremes of growth rate (Figure 1), rapid abbreviation of the tail commenced at about 60 days and 125 days respectively. In the former, the maximum length reached was smaller. However, in both samples, all larvae were longer than 33 mm before resorption of the tail began. A maximum length of 41 mm was measured. Post-resorption length was 11–13 mm ($\bar{x}$ = 12,4; *S.E.* = 0,5; *n* = 17), regardless of growth rate. Emergence of the fore-limbs occurred between one and three days after resorption of the tail had commenced.

The relationship between hind-limb length and total body length, may be divided into three successive phases

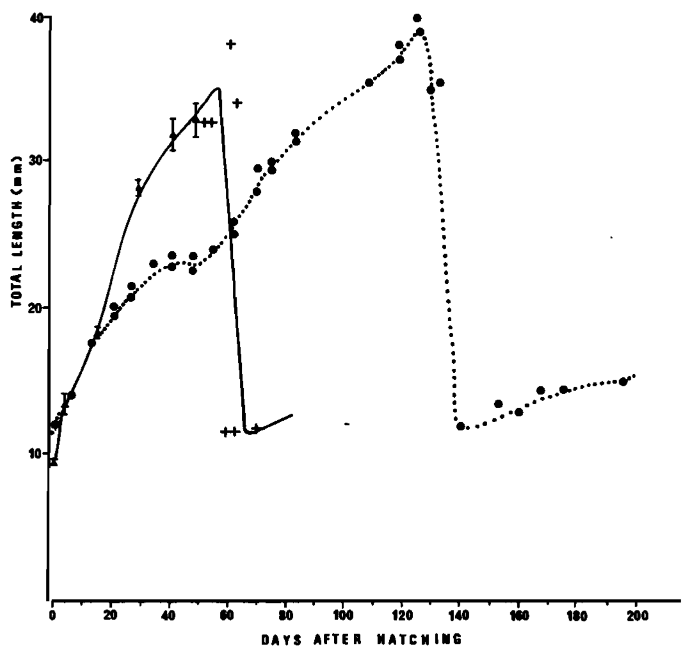

Figure 1 Variation in total length of *N. bonebergi*, from hatching to beyond metamorphosis, in three batches. Curves fitted by eye. Circles and crosses represent individual measurements from two batches of eggs. Triangles represent the means (with standard deviation) of between 6 and 11 individual measurements in a further batch.

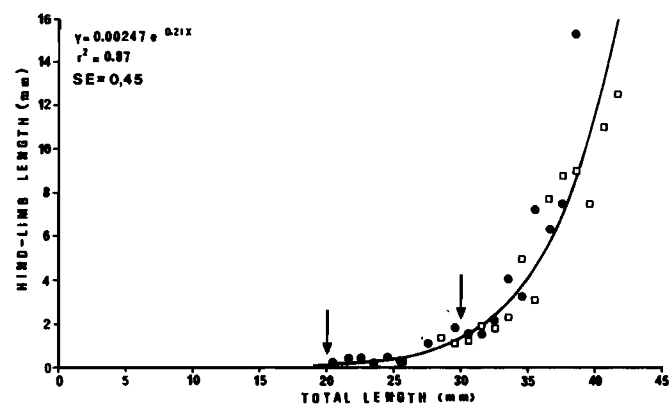

Figure 2 The relationship between total length and hind-limb length of *N. bonebergi* tadpoles. The points represent wild-collected (●) and laboratory-raised (□) populations (*n* = 46 and 47 respectively). Each point is a mean value. Arrows mark the limits of growth phases.

(Figure 2). During the first 10–12 mm of larval growth, up to a total length of 20 mm, the hind-limb buds had not yet appeared. After their appearance, initial growth was slow and the limb buds reached about 1 mm in length during the next 10 mm of larval growth. The last 10 mm of larval growth, up to the maximum length of about 40 mm reached at metamorphosis, is characterized by a rapid increase in hind-limb length, differentiation into its three component parts and increased pigmentation which begins dorsally in the 1,5–2,0 mm limb bud. Hind-

Table 1 Snout-vent length and limb lengths of reproductively active male and female *N. bonebergi*, collected in the Vernon Crookes Nature Reserve

	Males			Females		
	Snout-vent length	Hind-limb length	Fore-limb length	Snout-vent length	Hind-limb length	Fore-limb length
Mean (mm)	27	45	19	36	56	22
S.D.	1	2	1	2	5	2
Range (mm)	26–29	38–48	17–20	33–39	50–63	21–25
n	21	16	16	12	9	9

limb length at emergence of the fore-limbs is variable but may approach 16 mm.

Size at sexual maturity

Attempts to follow the development of post-metamorphic frogs to sexual maturity were unsuccessful. Most animals died about 20 days after metamorphosis and only one lived for 60 days. Sexually mature male and female frogs were collected in the Vernon Crookes Nature Reserve and subsamples of these were used to determine snout-to-vent length and leg length. The measurements (Table 1) are well representative of adult *N. bonebergi* occurring in the Nature Reserve.

Compared to the egg sizes of some highveld anurans (*cf.* Balinsky 1957), *N. bonebergi* eggs are large. Egg size directly determines tadpole hatching-size (Balinsky 1957) and large hatchling size is considered an adaptation to life in strongly flowing streams (Van Dijk 1971). Large egg size and hatchling size in *N. bonebergi* form part of a strategy to avoid the hazards of early development in an aquatic environment, a strategy typically found in the phylogenetically advanced reproductive mode of arboreal egg deposition (Duellman & Trueb 1986). The larger size (12,6 mm) at which some tadpoles hatched, is thus considered to be the norm. The smaller tadpoles probably hatched prematurely and, not being able to feed, would be less likely to survive than the stronger swimming, larger tadpoles which were ready to start feeding immediately.

The rate of larval growth was shown here to be variable. The shortest larval period reported is probably close to optimal. Most tadpoles measured routinely during experimental studies, developed more slowly and reached metamorphosis later, but more often reached a size of up to 40 mm before the onset of the metamorphic climax.

It is difficult to describe the rate of larval development in nature, owing to the daily release of tadpoles from egg masses over a period of months. Consequently no cohorts of developing tadpoles can be followed. Hind-limb size is useful since it gives an indication of the phase of tadpole development. Moore's (1964) indication of the boundary between pre- and pro-metamorphosis seems to be very arbitrary, and although we do not intend to indicate such a precise boundary, the phase of rapid hind-limb growth, characteristic of pro-metamorphosis, is nevertheless evident from our studies.

Although there was no apparent sexual difference in size directly after metamorphosis, males doubled and females trebled in length by sexual maturity. Poynton (1964) registered a maximum length of 37 mm which accords with our results and confirms that little post-metamorphic growth occurs compared with some other species (Balinsky 1969).

Wager (1931, 1952) did not succeed in incubating and rearing *N. bonebergi* tadpoles under laboratory conditions. Nevertheless, we succeeded in transporting egg masses from Natal to Bloemfontein, obtained a high percentage hatching and reared the tadpoles virtually without any mortality until post-metamorphosis. We have found the availability and easy rearing of *N. bonebergi* tadpoles especially valuable in experimental parasitological studies involving *Polystoma* spp. (Monogenea). *N. bonebergi* tadpoles served as natural or substitute hosts and the transparency of the ventral body wall (*cf.* also Wager 1931) facilitates observations of live parasites attached to the gills.

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