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'ASPECTS OF THE BIOLOGY OF THE COMMON FIJIAN SEA SNAKE *LATICAUDA COLUBRINA* (SCHNEIDER)'

by

MICHAEL L. GUINEA

IN FULFILMENT OF
MASTER OF SCIENCE

SUBMITTED TO
THE UNIVERSITY OF THE SOUTH PACIFIC
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ABSTRACT

Investigations into the biology of the banded sea snake, Laticauda colubrina, which inhabited various islands in Fiji, were conducted during the period, 1980 to 1982. Studies concentrated on the morphology, reproductive biology, and fluctuations in population size on a daily and seasonal bases. Toxicity studies were conducted using venom from captive snakes on mice and chick muscle.

1. Adult female superiority was demonstrated by snout-vent length (max = 143.5 cm) and weight (max = 1200 g). Adult males differed significantly from females in length, weight, shape and thickness of the tail, tail length, number of black bands, number of ventral scales, number of subcaudal scales, body scale rows at mid-body and vent, and the number of supralabial scales. The number of subcaudal scales displayed the greatest difference between the sexes and was used for sexing immature specimens.
2. Courtship and mating behaviour are documented. Seasonal reproduction was established for females by using ovary weight index, the size of the largest follicle in the ovary, and the presence of spermatozoa and oviducal eggs in the oviducts. Reproduction was confined to the summer months. Male reproductive cycles coincided with that of females. Eggs, laid in captivity, incubated at room temperature in 121-126 days. Eggs were not found in the wild.
3. Sexual maturity was attained by females at 26 months (s-v length = 98 cm). Males reached maturity at 15 months (s-v length = 70 cm).
4. The diet consisted of conger and moray eels, exclusively (Muraenesocidae and Muraenidae respectively).
5. Adult sex ratios varied from 2.4 : 1 (M : F) to 1.1 : 1 (F : M), but generally did not differ from 1 : 1.
6. Mark and recapture studies were conducted on Bausau Island where the winter population was estimated at 1106 by using a zero-truncated geometric distribution. The summer population of 1398 was obtained by using a zero-truncated Poisson distribution (Caughley, 1977). The percentage of the population which changed habitat per day decreased from 91 ± 1.8% in winter to 72 ± 10.2% in summer. This change of behaviour was assumed to be responsible for the change in catchability which was inherent in the methods used to estimate the size of the population.

7. While ashore, most snakes rested. Activity in the population was initiated by sunset, high tide and showers of rain.
8. Juvenile L. colubrina fell prey to portunid crabs on the reef flat. Predation on adult specimens was not observed. Mortality included fire, exposure, dehydration and other unknown causes.
9. The thermal preference for L. colubrina was about 30°C. The body temperatures of snakes in the water differed only slightly (max = 1.5°C) from the temperature of the water. Body temperatures of adults on land reached 7°C above air temperature and 5°C above ground temperature.
10. The morphology of the venom gland was documented and the functional fangs and teeth were examined. Mean fang length of adult females was 2.7 mm. The number of palatine, pterygoid and dentary teeth were in agreement with those given by Mao and Chen (1980). A single maxillary tooth was present behind the fang, for each skull examined.
11. The venom was a clear viscous liquid which formed a white solid when dried. The maximum volume of venom per snake was 78 µl and the maximum percentage solid was 41.8%. The percentage solid increased in those snakes deprived of water during captivity. Venom irreversibly blocked neuromuscular transmission in chick biventer cervicis nerve-muscle preparations. The LD_{50} was 0.35 mg/kg when injected (i.p.) into mice.
12. The implications of the investigations are discussed and areas for further research are outlined.

I. INTRODUCTION

Our present knowledge of the biology and systematics of sea snakes is indebted to the efforts of Malcolm Smith who in 1926 published his "Monograph of the Sea Snakes (Hydrophiidae)". The need for such a publication arose from the multitude of synonyms applied to specimens by different authors. Even the distinguished work of Boulenger (1898) was, in Smith's opinion, in need of revision. By examination of the specimens housed in all the great museums of the world, and from his collection of numerous specimens obtained during his travels, Smith distinguished, by his skilled observation and insight, 50 species and six subspecies of sea snake. He presented selected morphological characters for all of the specimens he examined. For each species he presented a list of synonyms and their authors, as well as a description of the species based on his observations along with notes on variation and distribution.

For almost five decades after Smith's (1926) monograph, studies on sea snakes were limited in scope, but included significant contributions by Bergman (1943) on breeding habits, Saint Girons (1964) on ecology, and McDowell (1972) on systematics. In 1975, William Dunson edited "The Biology of Sea Snakes" which, for the first time, presented a thorough account of contemporary research by many authors. This book produced considerable impetus to research into the biology of sea snakes, especially in the areas of natural history, ecology, physiology, venom, and their relationships to man.

Throughout Dunson's (1975) book, the need for further research was emphasised. It was pointed out that, although a great deal was known about the taxonomy and distribution of sea snakes from museum studies of records and specimens, little was known of the ecology of these animals. Dunson (1975 p7) commented on this aspect of sea snake biology: "Unfortunately, we know very little about how so many species can live in the same area without competing with one another. In large part, this lack of information may be blamed on the fact that sea snakes are tropical and biologists are not. In addition, there are few scientists dedicated enough to work on an animal whose bite may kill them".

In view of the limited information on sea snakes, and the abundance of Laticauda colubrina on some islands in Fiji, a study was initiated to investigate aspects of their biology. Established methods were employed in the investigations so that similar studies could be repeated in other areas, and meaningful comparisons could be made with existing literature to clarify ambiguities in systematics, biology and toxicology.

Previously published information on the sea snakes of the Fiji Islands were limited to locality reports (Smith, 1926; 1935), museum collections (Burt and Burt, 1932; Cogger, 1975), observations on the habits and morphology of _L. colubrina_ (Pernetta, 1977) and accounts of four species of sea snake (_L. colubrina_, _L. laticaudata_, _Hydrophis melanocephalus_ and _Pelamis platurus_) and their distribution in Fiji (Guinea, 1981). Tamiya _et al_ (1983) included data from Fijian specimens in the study of neurotoxic components of the venom of Laticaudidae.

Research was conducted throughout the latter part of 1980 until January 1982 on a part-time basis. The findings of that research into the biology and the toxicology of _L. colubrina_, are presented in this document. This thesis concentrated on _L. colubrina_ because of its large numbers on offshore islands and because of the dearth of information that existed, regarding all aspects of biology of this species. Previous studies on this species were fragmentary and, in places, anecdotal (e.g. Saint Girons, 1964).

Specimens of _Hydrophis melanocephalus_ were collected incidentally in the survey of coastal sea snake species. Because of their comparatively low numbers, and being almost strictly marine in their habits, the sample size remained small. _Laticauda laticaudata_ and _Pelamis platurus_ were also captured in very low numbers in Fiji and accounts of these have been published elsewhere (Guinea, 1981). The four species of sea snakes inhabiting Fiji are illustrated in Plates 1 to 4.

2. SYSTEMATICS AND ECOLOGY - A REVIEW

In spite of critical evaluation by many authors, the systematics of sea snakes is obscured by disagreement amongst authors as to the features which best display familial relationships. The diversity of opinion amongst herpetologists was demonstrated by Mao and Chen (1980) who listed six separate classifications proposed by seven researchers. As Mao and Chen (1980) remind us, the taxonomy of an organism should reflect its evolutionary relationships or phylogeny with other organisms. Sea snakes posed an interesting challenge. Being poisonous and front fanged (proteroglyphous) they were relatively late arrivals amongst the serpents (Smith 1926) and lack a meaningful fossil record. To complicate their taxonomy further, they display considerable adaptive radiations as well as probable convergence and parallelism (Mao and Chen, 1980). Since terrestrial elapid snakes and sea snakes seem to differ chiefly in the aquatic adaptations of the latter, several recent taxonomists have placed them in the same family, the Elapidae. Others treat them as separate families.

A cause of disagreement amongst authors is the position of the laticaudate group of sea snakes relative to the hydrophiid group. These have been labelled "false" and "true" sea snakes respectively. The laticaudine sea snakes possess a paddle shaped tail, as an aid to aquatic locomotion, and are front fanged as are the rest of the sea snakes. Yet, because of the lateral position of their nostrils, wide ventral scales and their egg laying mode of reproduction, they resemble some of the terrestrial elapids.

Smith (1926) in his pioneering monograph, classified all sea snakes into the family Hydrophiidae. Within this family he identified two subfamilies, the Laticaudinae and the Hydrophiinae. He considered the genus Laticauda to be the most primitive in the subfamily Laticaudinae which also contained two other genera, Aipysurus and Emydocephalus. The Hydrophiinae comprised the principal genus, Hydrophis, and closely allied genera. Smith (1943) proposed that Ephalophis was the common ancestor to the Laticaudinae and the Hydrophiinae.

The subfamily Laticaudinae was divided by Voris (1977). This produced a three-fold phylogeny, 1) Laticauda, 2) Aipysurus and Emydocephalus, and 3) Hydrophis and all the other genera. This implied either separate origins of the sea snakes or a single origin with separation soon afterwards.

McDowell (1972) shifted all the "true" sea snakes into the subfamily Hydrophiinae and placed the genus Laticauda into the Elapinae - a subfamily made up of terrestrial elapids. Both these subfamilies made up the family Elapidae. The genus Laticauda was thought to represent an independent marine derivative of the American and Asiatic coral snakes (Calliophis, Micrurus, Maticora) whereas the Hydrophiinae was derived from the Australasian elapids and most probably from the Demansia group. Burger and Natsuno (1974) agreed that the "false" sea snakes (Laticauda) and the "true" sea snakes had separate origins and placed the two groups into different families as Laticaudidae and Hydrophiidae respectively. The terrestrial elapids were placed in the family Elapidae.

Smith, Smith & Sawin (1977) proposed that the front-fanged, terrestrial elapids were closely linked with "true" sea snakes and these two groups of snakes comprised the family Hydrophiidae. They placed the genus Laticauda in the tribe Laticaudini within the subfamily of coral snakes, Elapinae, in the family of terrestrial elapids, Elapidae. Aipysurus and Hydrophis were separate tribes, Aipysurini and Hydrophiini respectively, within the subfamily Hydrophiinae which together with the subfamily of Australasian venomous elapids, Oxyuraninae, made up the family Hydrophiidae. According to their classification (Smith et al.,1977) the Proteroglypha, fixed front-fanged snakes, comprises two families - Elapidae and Hydrophiidae, each with a terrestrial subfamily and at least one tribe of marine snake.

Some authors (e.g. Harding and Welch, 1980) accepted the classification of Smith et al.(1977), but Cogger, Cameron and Cogger (1983) cautioned that further critical evaluation was needed, and adopted the more traditional classification of Burger and Natsuno. Cogger (1983) in the third edition of "Reptiles and Amphibians of Australia", referred to the families Laticaudidae, Hydrophiidae and to the family Elapidae. This elevation to family status for each group represented a significant departure from classifications used in the previous editions of his book and supported further Burger and Natsuno's classification.

Since this thesis is dedicated to a single species, it is not intended to contradict existing classifications. That proposed by

Cogger _et al._ (1983 i.e. Burger and Natsuno, 1974) is used because of its clarity. An updated list of authors and their classifications, including that given in Mao and Chen (1980 p1), appears in Table 1.

The confusion resulting from such differing taxonomies is likely to continue until the results of nonmorphological studies are complete. Mao and Chen (1980) conclude by stating "...[nonmorphological studies] proved that sea snakes are a natural group, quite distinct from the Asian terrestrial elapids, but closely related to the Australian elapids. The results achieved by these studies also show that _Aipysurus_ and _Emydocephalus_ have diverged only slightly from _Hydrophis_, and _Laticauda_ bears more affinity to _Hydrophis_ than morphological criteria indicate.".

Cogger (1985) and Tamiya (1985) shared the view that although definite familial classification of front-fanged snakes had not been possible using non-morphological characters, at their time of writing, potential lineages could be identified. The simplest classification outlined five groups, namely (1) _Laticauda_, (2) hydrophiine sea snakes, (3) Australasian elapids, (4) Afro-Asian and New World elapids and (5) mambas (_Dendroaspis_). Tamiya (1985) suggested that the hydrophiine sea snakes and the Australian terrestrial elapids may be combined into a larger group. Further discussion and speculation on taxonomy at this (family) level is beyond the scope of this presentation.

A. FAMILY LATICAUDIDAE

The Family Laticaudidae comprises a single genus with five species which are sympatric in parts of their range. They inhabit the tropical coastal waters of the Indian and Pacific Oceans. All species are amphibious to some degree and leave the water regularly. The broad ventral scales of the Laticaudidae enable them to move inland over rough terrain. One species, _Laticauda colubrina_, has been observed climbing vegetation in this study . Mao and Chen (1980) report collecting three specimens of _L. colubrina_ from the top of a solitary coral block 50 metres above sea level.

In general, all species of the genus are conspicuously banded and have attracted the common name of banded sea kraits. Although some individuals are more melanistic and therefore display less distinct banding. The females are larger than males, but have a relatively shorter tail. All species are oviparous and the eggs are deposited on land. Little is known about their mating behaviour, nesting sites and aquatic life. They feed on marine fish, most commonly eels, although McCoy (1980) states that L. colubrina possibly feeds on lizards in the littoral zone.

(i) Genus Laticauda Laurenti

Smith (1926) listed four species of Laticauda which he separated using the number of body scale rows, the presence or absence of the azygous prefrontal shield, the horizontal division of the rostral shield, ventral scale counts, the number of black bands and the general body colour including that of the upper lip. His key to the species of the genus Laticauda is reproduced in table 2 because it forms the basis of the keys produced by more recent authors e.g. Cogger (1975).

(ii) Distribution of species.

Harding and Welch (1980) list the species presented in Smith's (1926) monograph plus another identified more recently. The five species and their distributions (Harding and Welch, 1980) are listed below.

Laticauda laticaudata (Linnaeus)
Type Locality: India
Distribution: East India, Sri Lanka, China, Taiwan, Japan, Indonesia (Sumatra and Java), Philippines, New Guinea, Australia, Melanesia and Polynesia.

Laticauda colubrina (Schneider)
Type Locality: Unknown
Distribution: East India, Sri Lanka, Burma, Malaysia, Gulf of Thailand, Japan, Sumatra, Philippines, New Guinea, Australia, Melanesia and Polynesia.

Laticauda semifasciata (Reinhardt)
Type Locality: Moluccas
Distribution: China, Taiwan, Japan and the Philippines.

Laticauda schistorhynchus (Gunther)
Type Locality: Savage Island (= Niue)
Distribution: New Guinea, Melanesia and Polynesia.

Laticauda crockeri (Slevin)
Type Locality: Lake Tungano, Rennell Island, Solomon Islands
Distribution: Solomon Islands (type locality only).

(iii) Background.

Volsøe (1955) described a new subspecies, *Laticauda laticaudata wolffi*, from Lake Tungano, Solomon Islands. It was a melanistic species that inhabited the freshwater lake on Rennell Island. Some authors (Tamiya *et al.* 1983) now consider *L. laticaudata wolffi* to be a synonym for *L. crockeri* although Cogger (1975 p.124) cited a statement by Voris (1969 unpublished thesis) to the effect that "*wolffi* may represent the product of recent hybridisation between *crockeri* and the immigrant *laticaudata*".

Stejneger (1907) suggested that *L. schistorhynchus* was a separate race of *L. semifasciata* from the South Pacific. Apart from the differences in scale counts and the number of bands, the two species are morphologically very similar. The case for *L. schistorhynchus* to be relegated to a subspecies of *L. semifasciata* was supported by protein structure studies by Guinea, Tamiya and Cogger (1983).

Tamiya *et al.* (1983) recognised two distinct populations of *L. colubrina*. Those from the North Pacific (Japan and the Philippines) had significant genetic differences in the structure of the long chain neurotoxins, to those of the South Pacific (Solomon Islands, New Caledonia, and Fiji). This separation of populations based on morphological characters was reported by Guinea (1981). *L. laticaudata* is similarly divided into North Pacific and South Pacific populations (H. G. Cogger pers. comm., 1982).

The generalised distributions of the species of *Laticauda* given by Harding and Welch (1980) are somewhat misleading. Within the waters of the South Pacific, *L. crockeri* and *L. semifasciata schistorhynchus* are extremely localised. Although Smith (1926) lists a specimen of the latter from Bertrand Island, New Guinea and several from Tonga and Samoa, no specimen of *L. s. schistorhynchus* was recorded by Burt and Burt (1932) after extensive sampling throughout the Pacific region. The possibility exists that where *L. s. schistorhynchus* occurs individuals are gregarious and tend not to emigrate.

Minton (1975 p30) commented on the sympatry within *Laticauda*

"It is also of some interest that Laticauda colubrina and L. laticaudata, of much the same size and general appearance, are macrogeographically sympatric over an immense range while the two other quite similar species, semifasciata and schistorhynchus, are widely separated". Specimens of L. laticaudata have been recorded from Fiji (Burt and Burt, 1932; Cogger, 1975; and Guinea 1981) but they are not as common as they are reported to be in New Caledonia (Gail and Rageau, 1958; and Saint Girons, 1964). It is of interest that on Niue, L. laticaudata is sympatric with L. s. schistorhynchus. Voris (1972) reports a small fish (Eviota sp.) from the stomach of L. s. schistorhynchus. I have found juvenile surgeon fish (Paracanthurus hepatus) in stomach contents of L. s. schistorhynchus. As L. laticaudata feed on eels, there could be little competition between them. The interaction and competition between L. laticaudata and L. colubrina, which also feeds on eels, has not been documented.

Records of L. colubrina in Australian (Cogger, 1975) and New Zealand (McCann, 1966) waters in all likelihood represent waifs that have been carried by ocean currents south from the tropics. There is no account of L. colubrina breeding in or being a regular visitor to Australian waters. Sightings may be attributed to banded snake eels, Leiuranus semicinctus or Myrichthys colubrinus (family Ophichthyidae) (Plate 5), which are reported to be mimics of L. colubrina (Pernetta, 1977). The distribution of each species of snake eel as reported by Carcasson (1977) is greater than that of Laticauda the proposed model.

(iv) Ecology

(a) Laticauda colubrina

As Laticauda is not common in American and Australian waters, it has not received the research attention of other sea snake species in the current literature such as "The Biology of Sea Snakes" edited by Dunson (1975) yet provided a comparison for other sea snake species. Few publications on Laticauda were based on specimens which were collected by the author of such contributions. Valuable field information based on direct observation was given in Saint Girons (1964), Pernetta (1977) and Guinea (1981). Being field oriented, each contributed significantly to elucidating the ecology of the Laticauda.

Saint Girons (1964) presented his findings from visiting several localities in New Caledonia on two occasions (two months apart). He described the sympatry between L. colubrina and L. laticaudata on the same island and estimated the mortality of different age groups. His use of plastic tags enabled estimates the population using the islands to be calculated. The frequency of snakes moving from the sea to land was calculated from trails crossing the beach. The latter figure was interpreted as the frequency of feeding. The population structure was outlined and estimates of fecundity were given for the populations to remain stable. Seasonality in reproduction was suggested from a small sample of dissected specimens.

Pernetta (1977) presented observations on the morphology of L. colubrina from Fiji. His findings were based on collections from two localities at a months interval. He presented a list of eel species removed from the stomachs of the individuals he collected. Males fed on smaller eels found on the reef crest while females preferred larger eels of different species from deeper water. He suggested that reproduction was seasonal with several clutches deposited throughout the summer. He discussed speciation within Laticauda and presented statistical analysis of taxonomic features. Mimicry was postulated, with L. colubrina being the model and the banded snake eel being the Batesian mimic.

Guinea (1981) presented the morphometrics of reproductively mature L. colubrina from Fiji. Information on clutch sizes was given as well as the size and probable age of maturity for each sex. The number of prey species given by Pernetta (1977) was increased. The introduced mongoose Herpestes auropunctatus has restricted the distribution of L. colubrina to offshore islands and to other mongoose-free areas.

Gorman, Licht and McCollum (1981) described the annual reproductive pattern of L. colubrina from the Philippines. The specimens, of which the majority were males, were purchased from collectors in the Philippines. This method of collection may have affected his sample. Results from plasma steroid and testes weight analyses indicated, at least in the Philippines, L. colubrina was "probably completely aseasonal in its reproductive biology" (Gorman et al., 1981 p335).

(b) _Laticauda laticaudata_

This species has received little scientific attention, possibly because of its low numbers in Fiji. Smith (1926) gave scale counts for two specimens from the Fiji Islands, namely B.M.56.9.4.53 and U.S.N.M.5588. Burt and Burt (1932) recorded two specimens from Fiji (Cikobia, No. 29006 and Vanua Kula No. 40453). Cogger (1975) listed a specimen from Fiji (A M 6698) but on close examination of the number of ventral scales and the number of bands, I concluded that the locality for the specimen was in doubt. A single specimen was reported in Guinea (1981) from Toberua Island, Fiji. It appeared that this species was present in relatively small numbers in Fiji. Saint Girons (1964) and Mao and Chen (1980) reported the ecology of _L. laticaudata_ was similar to that of _L. colubrina_ in that both were found along rocky coasts or islands off the coast and fed mainly on small eels. A detailed investigation into the ecology of these two similar sympatric species could prove worth-while.

8. FAMILY HYDROPHIIDAE

The family Hydrophiidae comprises about 50 species of marine snake (Voris, 1977) which have anterior non-rotatable fangs, neurotoxic venom and specialised marine adaptations including flattened oar-like tails and nostrils positioned on the top of the snout and give birth to live young. Their ventral scales are reduced in size and often keeled. They are entirely aquatic in their habits and frequent coastal marine environments. Being benthic feeders yet air breathers, their distribution reflects the depths to which they can dive. This is usually where water depths are less than 100m. The greatest number of species exist on the continental shelf regions of S.E. Asia and Northern Australia. The number of species decreases with distance from this region. Novikov and Khomenko (1974) recorded five species from the west coast of India. Eighteen species of hydrophiid were recorded from India in general (Witaker, 1978). Ten species (excluding _Laticauda_) were recorded from New Caledonia (Laboute and Magnier, 1979). Mao and Chen (1980) record three species from Taiwan. Two species were recorded from

Fiji (Pernetta, 1977; Guinea, 1981).

(i) Genus *Hydrophis* Latreille

Smith (1935) described a single specimen of *Hydrophis belcheri* from Suva Harbour. This specimen was later reidentified by McDowell (1972) as *H. melanocephalus*. Pernetta (1977) records Dr. H. Cogger's comments on the Fijian specimens "... are comparable to Australian *H. melanocephalus* but differ from the nominate race". Cogger (1975) suggested that the Australian specimens may represent an undescribed taxon.

(ii) Ecology

(a) *Hydrophis melanocephalus*

McCosker (1975) recorded *H. melanocephalus* as the species which fed at the greatest depth (50 m) at Ashmore Reef, Australia. Yet in Fiji, *H. melanocephalus* was commonly found in shallow waters. Thirty specimens were collected as part of the overall study of sea snakes, from the shores of Laucala Bay at depths of less than one metre. Adult female specimens have been seen in Nabukulau Ck. which flows through Suva, but most sightings came from the intertidal sea grass beds (*Syringodium isoetifolium*, *Halophila minor* and *Halodule pinifolia*) from around Suva Peninsula and Bau Waters.

Sand eels (*Callechelys melanotaenia*) and snake eels (*Lieuranus semicinctus* and *Myrichthys colubrinus*) were the predominant prey species (Guinea 1981). Observations on the feeding behaviour reported by Guinea (1981) were supported by Takahashi (1981). The small head and slender neck of the species enabled it to burrow the anterior section into the sand and maintained this position by bracing the broad tail and posterior of the body into the swell.

Reproduction was seasonal as was reported for other species of hydrophiid (Bergman, 1943; Limpus, 1975 and Voris and Jayne, 1979). Juvenile specimens (s-v length < 40 cm) were found from March to June in Laucala Bay. The number of young in a clutch varied from one to eight. Mao and Chen (1980) report breeding by this species in August and September in Taiwanese waters. Little has been written about this species and further research is in order.

(iii) Genus Pelamis Daudin

This is the most widely distributed of all sea snakes. Unlike other species Pelamis is totally pelagic. It is recorded from the east African coast and through the Indian and Pacific Oceans to the west coast of Central America. The genus comprises one species made up of several races (Kropach, 1975). Instead of the banded pattern of many sea snake species, the dorsal half of the body is black and the lower half yellow. The tail is spotted. In colouration and distribution it is a most distinctive species and the only sea snake likely to be encountered in the open ocean. It feeds on surface water fish which are apparently deceived by its appearance and approach it for protection.

In Fiji a single specimen was found in Laucala Bay after a cyclone in 1979. I captured two specimens ten nautical miles South of Suva. The snakes were attracted to the flood lights of the "Tavuto" which was operated at night by the Department of Fisheries for feasibility studies of a squid fishery. The number of specimens examined during the survey was small because of the difficulty of obtaining specimens from the open sea on a regular basis.

3 DESCRIPTION OF STUDIES

Initial investigations into the seasonal patterns of reproduction involved locating the areas frequented by L. colubrina. There were no large concentrations on Suva peninsula, but individuals were collected from several localities including the storm-water drains beneath Suva city, crevices in rock retaining walls at Lami, and from crevices in the jetty at USP. However, a survey of the islands within Laucala Bay, Bau Waters and to the west of Suva revealed substantial populations. These populations were used to investigate

a) the seasonality of reproduction,
b) the seasonal fluctuations in population size and composition,
c) fecundity and sites of egg deposition,
d) the growth rates of juveniles,
e) the diet and the duration spent on land,
f) the temperature ranges for active animals.

Information on size, sex ratios, scalation and colour was recorded during visits to the islands and also from the specimens which were collected for dissection. This provided a large data base of variation in morphological characters from the populations of S. E. Viti Levu.

Diel behaviour patterns were documented during different seasons by observing the movements of individuals after they came ashore. Sausau Island north of Vanua Levu proved to be the best locality for such observations and provided a site for comparative population studies.

A. THE STUDY AREAS.

Pernetta (1977) collected specimens from Makaluva and Mabualau. During this study Makaluva was not included as a collecting site as no specimens were seen on the island in spite of regular visits. Observations on L. colubrina were made on the other offshore islands of S.E. Viti Levu (Figure 1). Regular samples of the populations were collected from Mabualau and Toberua in Bau Waters and from the islands of Namuka and Vuiva to the west of Suva.

Toberua Island has been cleared for a tourist resort but the others support thick vegetation. Mabualua, a small uplifted limestone island, provided ample shelter for the snakes in the honeycombed erosional features of the rock. Namuka and Vuiva Islands were composed of marl and sandstone similar to the neighbouring areas of the mainland. On the leeward side of Namuka stood a derelict ship's boiler which was used by L. colubrina throughout the year. With the exception of Toberua, these islands are surrounded by fringing reef-flat which limited access to the island except at high water.

Observations on population structure and behaviour were made on Sausau Island (16° 16' South, 179° 27' East) in the rain shadow of Vanua Levu (Figure 2). This volcanic island supported a variety of terrestrial habitats as well as mangroves and exposed beaches. Being in the rain shadow produced a marked seasonality in rainfall when compared to the wetter islands of S. E. Viti Levu, yet monthly mean temperatures were similar (Figure 3). Sausau was an excellent island for observing individuals during their time on land. The population was large (about 100 different individuals were caught each day) and in the most densely populated areas there were not the numerous crevices and recesses as were present on Mabualau.

B. METHODS

The study areas of S.E. Viti Levu were visited at least monthly during the period of the research. January was the only month not sampled. Visits were of several hours duration and usually lasted from high water to the next high water. This allowed boat access across the fringing reef. On each trip an assessment of abundance and activities of the snakes was made prior to the collection of specimens. It was neither feasible nor possible to capture nor to collect all the snakes sighted. Collections representative of the population were made on the basis of sex, size and activity: e.g. leaving the water, basking, mating etc.. Specimens were captured by hand. They were sexed, measured and the cloacal temperature recorded. The majority of snakes were released at the site of capture but a sample of at least eight were brought back after each trip to the laboratory at USP.

A number of specimens were collected from Toberua Island by the island management. These were brought to the laboratory and formed the collection from Toberua for that month. Snakes returned to the laboratory were usually killed by freezing and kept at -10°C until ready for dissection. When freezer facilities were not available, specimens were injected in the region of the heart with sodium pentobabarbitone and preserved in 10% Formalin solution. Captive females with obvious, enlarged ova were kept alive in cages until after egg deposition or until they lost "condition" after which they were sacrificed for dissection. A group of 16 snakes were kept alive and used for venom collection over a period of four weeks.

4 MORPHOMETRICS

A. INTRODUCTION

Smith (1926) described L. colubrina as having 21 to 23 scale rows at the neck and 21 to 25 at the mid-body. The scales were imbricate and smooth throughout. The ventral scales numbered between 213 and 245 with each being four times as broad as it was long. The anal scale was divided and there were 37 to 47 subcaudal scales in the males and 29 to 35 in the females. The azygous shield separating the prefrontals was absent at times. He stated that the black bars on the body varied in width and number but was unable to correlate the variation with geographical distribution.

The description given above included six specimens from Fiji. Pernetta (1977) provided morphometric data for 29 specimens also from Fiji. Saint Girons (1964) gave similar data for 7 specimens from New Caledonia. Mao and Chen (1980) presented data for 23 specimens from Taiwan. The lack of morphometric data from a large number of specimens from a single geographic location stimulated a more thorough investigation of this aspect of the L. colubrina population in Fiji.

B. MATERIALS AND METHODS

Selected morphological measurements were obtained by the following methods.

The snout-vent length (s-v length) was measured to the nearest 0.5 cm using a flexible fiberglass tape.

The length of the tail was measured to the nearest 0.5 cm, from the vent to the tip of the caudal scale using the same tape.

The number of black bands was counted on the ventral surface. The most anterior band when viewed dorsally was commonly incomplete on the ventral surface and joined the black markings on the head. Its union on the ventral surface was recorded but was not included in the band count.

The colour of the tip of the tail was noted as being either black or white, with white being the absence of pigment in the caudal scale when it was held to the light.

Ventral scales were counted from the most anterior enlarged scale on the ventral surface to the anal scales. Notes were made as to the position and the nature of any scale abnormalities.

The position of the umbilical scar, when obvious, was noted as a ventral scale position from the anterior.

The number of pairs of subcaudal scales was recorded from the post anal scales to the caudal scale.

Body scales were counted in three places along the body. At the first position, the count started at the most anterior ventral scale and continued around the specimen from right to left. The second position was at the mid-body i.e. half the s-v length. This was in the region of the 100th ventral scale. The final count was from the last ventral forward, from left to right. Samples were selected indiscriminately for a count of body scales starting in the same position but in the opposite direction. The intervening number of ventral scales between the start and the finish of each body scale count was noted in each case.

Shields on the head were counted. The presence or absence of the azygous shield was noted for each specimen. Any division or aberration of the rostral scale was recorded.

Both infralabials and supralabials were counted on each side of the lower and upper jaw respectively.

The data were recorded as disk files using an Apple IIe computer with 64K of RAM. All programmes were written in Applesoft BASIC by the author and tested for accuracy using examples from "Biostatistical Analysis" by Zar (1974). Yates correction was used with all Chi square tests where the degrees of freedom equalled one.

C. RESULTS

The differences between male and female specimens of _L. colubrina_ have been recorded by Pernetta (1977) and his findings were supported by this investigation. Mature females were larger in body weight and s-v length than mature males. No males were longer than 100 cm in this study yet females had just reached sexual maturity at this size (see chapter 5). The shape and thickness of the tail was the most obvious difference between adult males and females. In males, the tail was enlarged ventrally to accommodate the hemipenes. This produced a pear-shaped cross section in contrast to that of the females which were of uniform thickness (Plate 6).

(i) Description of specimens.

A male and a female specimen were selected for a detailed description of their morphology and positions of organs. These specimens are housed in the Reptile and Amphibian Collection of the Fiji Museum, Suva. Their catalogue numbers are RA224 (female) and RA189 (male). The results of this morphological and anatomical comparison are presented in Table 3.

Mao and Chen (1980) gave a description of a female specimen from Taiwan. From their description few differences were discernible except for the numbers of ventral scales and black bands. These features are discussed further in this chapter. Data on the position of organs were given so that should more information from other localities become available then meaningful comparisons may be made. The left lung was reported to be vestigial in the Taiwanese specimen, but McCarthy (1982) stated that this character was present in some L. colubrina specimens. This character was not observed in the Fijian specimens presented in Table 3.

(i) Single Character Analyses.

Unless indicated otherwise, the following descriptions refer to specimens from S.E. Viti Levu.

(a) Bands.

A sample of 226 specimens were examined to estimate the frequency with which the most anterior black band was joined ventrally. Of the males, 1% had this band joined as did 9.5% of the females. This revealed a significant difference between males and females (Chi^2 = 5.99, dof = 1, $P < 0.025$). As this band was more commonly joined in females than in males and as it joined the black markings on the head, it was omitted from the black band count for the body.

(b) Rostral Scale.

In *L. colubrina*, the rostral scale was intact and normally showed no division (Smith, 1926). The horizontal division of the rostral scale was a distinguishing feature of *L. semifasciata* and *L. s. schistorhynchus*. Within the *L. colubrina* population of S. E. Viti Levu, 318 specimens were examined for this character. All 131 males had the rostral scale intact. However, four females (2.1%) exhibited a horizontal division of this scale. This difference between the sexes was not significant (Chi^2 = 1.39, dof = 1, $P < 0.25$). The presence of this character within the species, even in such low frequencies is interesting and could represent an ancestral vestige.

(c) Caudal Scale.

The colour of the caudal scale was recorded for 322 specimens. White caudal scales were found on 43 males (31.4%) and 33 females (17.8%). The remainder had some dark colouration when held to the light. The difference in this character between males and females was significant (Chi^2 = 7.32, dof = 1, $P < 0.01$).

(d) Azygous Scale.

The presence or absence of the azygous scale between the prefrontals was recorded for 327 specimens. Of the population, 4.6% lacked this scale. There was no significant difference between males and females (Chi^2 = 1.38, dof = 1, $P < 0.25$). The absence of the azygous scale is a characteristic of *L. laticaudata* and *L. crockeri*. The specimens examined above, displayed typical *L. colubrina* features for all other specific characters, including the colour of the upper lip and the number of body scale rows. Pernetta (1977, p1614, table 2) presented a table of the morphometric variation in *L. colubrina* from Fiji, which in part read;

"% with median	6%	8%	9%	-
prefrontal scale	(1)	(1)	(1)	"

I assume the heading should read "% without median prefrontal scale". After such an alteration our results would be in agreement.

(e) Sexual Dimorphism.

Figure 4 (a - l) presents the bar graphs of morphometric data for male and female specimens from S.E. Viti Levu. Table 4 gives, for each sex, the mean, standard error and range for the parameters tested. Geographic variation could not be detected between specimens from different islands.

The majority of parameters chosen gave a significant difference between the sexes. The results of statistical analyses on all the parameters measured are given in Table 5. The following gave a significant difference between males and females at the 95% confidence level when analysed using a median test with Chi square analysis and analysis of variance test; snout vent length, tail length, number of black bands, number of ventral scales, number of subcaudal scales, weight, body scale rows at mid-body and vent and the number of supralabial scales. The parameters which revealed no significant difference between males and females were the position of umbilical scar, the number of body scale rows at neck and the number of infralabials.

(ii) Aberrations in Scales.

(a) Body Scales.

A sample of 32 males and 34 females were used to investigate the amount of scale row aberration in the region of the counts. The major form of aberration occurred when the count of scale rows around one side of the animal did not equal the count around the other or, if the number of scale rows were equal, the count finished on a different ventral scale. The unequal counts of body scales around each side of the animal indicated the division or union of scale rows. Counts along a row that divided to form two rows gave either, a count equal to that of the other side, but terminated at the ventral scale anterior to where the previous count finished, or alternatively gave an equal intervening ventral scale count but gave a larger body scale row count. Counts across such a row gave a larger scale row count and a larger number of intervening ventral scales.

The percentage of specimens that had an equal number of scale rows around each side of the body is shown in Table 6. Males displayed less aberration at the mid-body than at any other position. Females had the minimum amount of division occurring at the neck. The frequency of unequal scale row counts was not significantly different for males and females (max. $Chi^2 = 2.6$, dof = 1, $P < .05$).

The most frequently occurring (modal) values for scale row counts at different parts of the body are shown in Table 7. In general, males deviated less from the modal value than did females. The one exception was the bimodal frequency of scale rows at the neck for males where 77% of the sample had 21 or 23 rows. A count of 21 body scale rows commonly had 11 intervening ventrals. Counts of 23 and 25 had 12 and 13 ventrals respectively. The regression equations calculated by the least square for the three positions on the body are presented in Table 8.

(b) Ventral Scales.

The ventral scales were normally large, single and extend across the ventral surface. In the region of the 200th scale from the anterior, one to five scales usually displayed a median division. On newly hatched animals this was the site of the umbilicus which joined the embryo to the extra-embryonic membranes. In 69 of the 71 adults examined the umbilical scar remained obvious. The position of the umbilicus from the anterior was not sexually related. However, because males possessed fewer ventral scales, it occurred closer to the vent in this sex. The difference of five or six scales from the vent was indicative of the difference in ventral scale counts between males and females.

Ventral scales were in some individuals divided in an irregular manner. Some individuals had half a ventral scale in a position which normally contained an entire scale. The corresponding half was found, usually, elsewhere along the body (Plate 7) so that the count of ventrals along one side of the body equalled the count along the other side.

(c) Labial Scales.

Males displayed less deviation from the mode than did females for infralabial and supralabial scale counts. Division of the labial scales was common in the females . This caused large and irregular numbers of scales to be recorded. The modes and their corresponding percentages are shown in Table 9. Males differed significantly from females in the number of supralabial scales but did not differ in the number of infralabial scales (Table 4).

(iii) Paired Character Analyses.

Relationships between characters were investigated to determine whether they varied with the size and therefore the age of the specimen. Where characters were independent of size, it was assumed that variation was due to the sex of the specimen. Snout-vent length was chosen as the independent variable and likely dependent variables such as ventral scale count and number of black bands were analysed to determine whether there existed a positive correlation. Figure 5 (a - g) presents graphically the relationship between the independent and other variables.

Snout-vent length was chosen as the independent variable likely to change with age and the dependent variables tested were the numbers of; (a) subcaudal scales, (b) ventral scales, (c) black bands and (d) tail length, and (e) weight. Tail length was used as the independent variable for a comparison with the number of subcaudal scales. The number of ventral scales was used as the independent variable to test their relationship with the number of black bands. The respective regression equations and correlation coefficients are given in Table 10.

A high degree of correlation was demonstrated for s-v length, both male and female, against weight and tail length. This was understandable as larger snakes were heavier and had longer tails. The poor correlations (less than 0.75) obtained by the other variables tested indicate that the numbers of ventral scales and black bands were independent of the size, but determined by the sex of the individual. For either sex, there was no obvious relationship between the numbers of ventral scales and black bands. The number of subcaudal scales was independent of the s-v length of the specimen and the length of its tail. The number of subcaudal scales varied with the sex of the individual and remained unchanged throughout its life.

D. DISCUSSION

(i) General Morphology.

In Fiji, L. colubrina was, typically, a conspicuously black banded sea snake whose colour between the bands may be white or cream. A few specimens from Mabualau had orange between the bands. Orange pigmented females sloughed their skins in captivity to reveal the normal white colouration between the bands. The orange pigment was possibly caused by a natural dye from decaying vegetation on the island. Females attained a maximum size of 143 cm. Males were considerably smaller (max. s-v length = 97 cm). The tails of both species were about the same length yet made up about 10% of the s-v length in females and 15% in males. Females, generally, had fewer bands than did males but no specimen possessed more than 38 black bands. Females had more ventral scales (222 to 238) than did males (218 to 230), but possessed fewer subcaudal scales, 27 to 38 and 37 to 46 respectively. The number of subcaudal scales displayed the greatest sexual dimorphism and was useful in determining the sex of immature specimens. The majority of adults retained the umbilical scar in the region of the 200th ventral scale. The number of scale rows around the body varied between 21 and 25 at the neck and mid-body. No specimen had 19 which was a feature of L. laticaudata. Females displayed more division of the supralabial and infralabial scales than did males. This last feature was considered to be an inadequate taxonomic character.

(ii) Colouration

Fijian specimens had 67% fewer bands than those reported by Mao and Chen (1980) from Taiwan. Records from New Caledonian specimens (Saint Girons, 1964) indicated they had a similar banding pattern to those in the present study. The significance of banding remains poorly understood. Two possibilities were outlined by Shine (1980b) for the burrowing snake Vermicella annulata; (i) it was aposematic and warned potential predators and (ii) it functioned to confuse potential predators by creating a visual illusion "flicker fusion" when the snake moved rapidly in dim light. Both possibilities applied to L. colubrina. Heatwole (1975) documented experiments conducted to demonstrate the effect of aposematic colouration on predators. Pernetta (1977) outlined a model for Batesian mimicry with the banded snake eels. When evading capture, L. colubrina undulated their bodies so rapidly as to adopt a side-winding mode of locomotion. While escaping, they were difficult for the author to see, because they appeared to be uniformally grey in colour.

A third explanation for the banded colouration has to do with basking. Resting individuals often had only a few bands exposed to the sun at any one time. Their bodies moved at intervals to expose fresh areas to the light and to heat other parts of the body. This is discussed further in Chapter II on temperature relations.

(iii) Ventral Scales.

The number of ventral scales was 96% of those reported by Mao and Chen (1980) from Taiwan. Voris (1975) reported a one-to-one ratio between ventral scales and vertebrae for L. colubrina. As the number of vertebrae can be increased by high incubation temperatures, a possible explanation for the difference between north Pacific and south Pacific populations, depends on the temperatures of the microhabitats in which the eggs incubate. As the actual site of deposition remains undocumented, such speculation is yet to be verified.

The number of black bands and the number of ventral scales were consistently less for South Pacific populations of L. colubrina, L. laticaudata and H. melanocephalus when compared with populations of each respective species from the North Pacific. L. s. schistorhynchus was distinguished from L. semifasciata by having fewer bands and ventral scales (Smith,1926). All four species belonging to two families of sea snake showed a parallel increase in the number of bands and ventral scales with increase in latitude in the North Pacific. Figure 6 displays the variation in the number of bands and ventral scales for L. semifasciata, L. colubrina, L. laticaudata, and the hydrophiid, H. melanocephalus, from South Pacific and North Pacific populations.

Figure 5(g) indicated that there was little relationship between the number of bands and the number of ventral scales of _L. colubrina_. Yet Figure 6 displayed a change in these characters with locality. Limited data are available on these species in intermediate localities e.g. Indonesia. De Rooij (1915) presented details for a number of species from Indonesia, but her form of presentstion prevented their inclusion in the above discussion. Beneficial information regarding a possible cline in these species could be obtained if De Rooij's specimens were re-examined.

(iv) Ventral Scale - Body Scale Relationship.

The relationship between the number of body scale rows and the number of intervening ventral scales between the start and the finish of the count appeared to be relatively constant for _L. colubrina_. Comparisons were made with the same counts for specimens of _L. s. schistorhynchus_ collected from Niue. Regression equations were calculated for the scale counts in question at three positions on the body (neck, mid-body and vent) for both species. The equations and their respective correlation coefficients are presented in Table 8 for _L. colubrina_, _L. s. schistorhynchus_ and for both species combined. The gradients (b values) differ only slightly for the three cases. Together with a strong positive correlation in each case, it can be assumed that the pattern of scalation (body scale rows : intervening ventrals) has a common lineage in these two species and is a generic character of _Laticauda_.

5 REPRODUCTION

A. INTRODUCTION

The reproductive biology of Laticauda has received little attention in the past. All species are oviparous as mentioned earlier (Chapter 1). Their eggs are deposited on land, although the exact location was not found during this study. Smith (1930) recorded ovoviviparity in a specimen of L. colubrina which contained well-developed embryos enclosed within a thin semi-transparent covering. Smedley (1931 a and b) reported that on the islands near Singapore, L. colubrina laid their eggs in rocky crevices where females protected the eggs and young. The eggs were laid in June, July and August. The average clutch size for eggs laid in captivity was six (Smedley, 1931b), but incubation attempts were unsuccessful. Smedley concluded that oviparity and ovoviviparity existed within L. colubrina populations. The mode of reproduction was determined by the accessibility of land, or possibly, by a local preference in Singapore for oviparity.

Herre and Rabor (1949) reported sea snake eggs in intertidal limestone caves on Gato Island, Philippines. Their report reads as follows;

"The caverns are in total darkness, but are well supplied with air through the many crevices and holes in the roof. By using flash-lights and lanterns large numbers of snakes may be seen lying about on the walls and floor of the caves. In small crevices and on the roughness of the walls lie strings or clusters of white snake eggs." (Herre and Rabor,1949, p283).

Such potential nest sites were rare in the study areas. Those that did occur were either so small as to prevent human entry or so open as not to allow a microclimate suitable for incubation to be maintained.

Saint Girons (1964) assumed the eggs were laid in sand. However, after careful examination of the sand areas on the islands of S.E. Viti Levu and Sausau, none of the disturbances in the sand were attributed to L. colubrina. Every disturbance in the sand that could have been a nest site, was excavated to a depth of 50 cm without finding any eggs or remains of such. It is likely that L. colubrina is a communal nester similar to Demansia psammophis (Covacevich and Limpus 1972) which, until the accidental unearthing of a cache of eggs, had similar uncertainty attached to their site of deposition.

To identify the seasonality of reproduction in Fiji a detailed study of the reproductive biology of L. colubrina was undertaken using specimens collected throughout the year from the study areas close to Suva. Mating in L. colubrina occurs on land and was first reported by Guinea (1981). A courting group (1 female and 2 males) of L. s. schistorhynchus was observed mating in the sea at Niue in March 1982. Details on courtship and mating of other species of Laticauda are not available.

B. MATERIALS AND METHODS

Snakes were collected as described in Chapter 3. Noticeably gravid females were maintained in the laboratory until parturition. Other specimens were killed within eight hours of collection and frozen until ready for dissection. After thawing to room temperature each specimen was dissected by an incision in the ventral body wall from the region of the heart to the anal scales. Records were kept of the sex, weight and s-v length for each individual and the weight of its stomach contents, if any.

(i) FEMALES.

Records included the size and number of ovarian follicles, corpora lutea (when distinguishable), the weight of the ovaries and the size, number and weight of oviducal eggs and the weight of fat present in the body cavity and the presence of spermatozoa in the oviducts.

The maximum diameter of the ovarian follicles and oviducal eggs were measured to the nearest 0.1 mm. The values for each ovary were recorded separately and later combined to produce a frequency histogram of follicle size for each specimen. In all, 68 histograms were produced for as many specimens. The follicles were divided into six classes based on their maximum diameter. The limits to a class were determined by the follicle diameters which consistently had the smallest frequencies (Betz, 1963; Zug, Hedges and Sunkel, 1979).

(a) Ovary Weight Index.

Shine (1977) used the combined ovary weight as a proportion of the body weight as an indication of reproductive readiness for terrestrial Elapids. This method was employed in the present investigation. The ovary weight index was calculated by dividing the combined wet weight of both ovaries by the net body weight and multiplying the result by 100. The net body weight was the gross body weight minus the likely temporary and seasonally variable weights which included the weight of the stomach contents, body fat and the oviducal eggs.

(b) Presence of Spermatozoa.

Data on the presence of spermatozoa were obtained by severing the oviducts a short distance in front of the cloaca and smearing their contents onto a microscope slide. After air drying and fixing over a flame, the preparation was stained with methylene blue, rinsed with tap water, air dried and examined under a microscope. If spermatozoa were present in any of the fields of view, the result was taken as positive. If no spermatozoa were observed after at least ten fields of view were examined, a negative result was recorded. No attempt was made to give a subjective estimate of spermatozoa abundance.

(c) Size at Sexual Maturity.

In order to establish the size of the females when they reached sexual maturity, 32 females of different sizes which were collected at intervals throughout the year had silicone moulds taken of their cloacas. All the specimens were killed by freezing and were later thawed for the investigation. The cloacal cavity was washed and swabbed with detergent to prevent the skin from adhering to the mould. Silicone sealant (Dow Corning 780) was inserted through the vent using the applicator gun supplied. Care was taken not to over-fill or distort the cloacal cavity; excess silicone was allowed to escape through the vent and also into the rectum so that the resting shape of the cavity could be recorded in the mould. The silicone was allowed to set for several hours.

The mould was eventually dissected out and the excess silicone trimmed away. The weight of the mould showed little relationship to body weight or to any other parameter. The distance between the urinary papilla in the median dorsal position in the cavity (clearly visible as a depression in the mould) and the septum between the oviducts (clearly visible as major depression in the anterior of the mould) was taken as a reliable measurement and free from distortion and artifacts in the procedure. The straight line distance between these two points was measured with a vernier calliper to the nearest 0.1 mm.

(d) Eggs and Clutch Size.

Clutches laid in captivity were removed for incubation trials. Individual eggs were measured and weighed and placed in containers with conditions similar to those that might be experienced in the wild for their incubation. Eggs were covered with sand moistened with fresh water and left to incubate at room temperature. Others were covered with sand moistened with sea water and again left at room temperature to incubate. After several unsuccessful attempts to incubate the eggs, a group of seven were given a light sprinkle of tap water and placed inside a loosely sealed plastic bag, and left to incubate at room temperature.

(ii) MALES

Dissection records for the male snakes included the weight of fat in the body cavity and the weight of the testes. Gorman _et al._ (1981) reported temporal patterns in testis size based on length, width, calculated volume and weight were the same for the three species of sea snake from the Philippines. Zug _et al._ (1979) used the proportion of testis length to s-v length as an indicator of reproductive status for three species of Central American land snake but concluded that " weight or volume [of testis] would have been more indicative " (Zug, _et al._, 1979, p2). Shine (1977) used the combined testes weight as a percentage of body weight to produce a testis weight index. This latter method was employed in this investigation.

(a) Testis Weight Index.

The testis weight index was calculated as the ratio of the combined (wet) weight of both testes, to body weight (minus stomach contents and body fat), multiplied by 100. Shine (1977) pointed out the need for the testes weight index to be independent of body length for this ratio to be justified. In the present study, when the monthly sample size exceeded three, regression analyses of testis weight index and s-v length, revealed a zero gradient in each case.

(b) Hemipenis Characters.

Each hemipenis was everted and examined for soil adhering to it and inflated with water to full extension and measured to 0.1 mm with a vernier calliper as follows:

(1) the tip to tip distance (distance between the sulcus spermaticus),

(2) the maximum diameter (usually at the distal end),

(3) the length of the calyculate area (distal end),

(4) the length of the spinous area (proximal end).

The values obtained for left and right hemipenis were averaged to produce a single value for each parameter for each specimen. The presence of soil on the shaft of a hemipenis was thought to indicate the specimen had been recently sexually active, until a male was observed protruding its hemipenis on land while it was basking.

C. RESULTS AND OBSERVATIONS

(i) Courtship and Mating

Observations on mating were first made on Mabualau Island on 26th October 1980 (time = 15:30 h, daylength = 12 h 40 min, ground temperature = 27.0°C.) This followed a six week period of cool wet weather which had changed the previous day to warm and sunny. The specimens (female s-v length = 99.5 cm and male s-v length = 79.5 cm) were in a cleared shady area 20 m inland from the high water mark (Plate 8).

As summer approached, courting pairs became more common and several complete courtships were documented on Sausau Island. The majority of successful matings took place in the early evenings either during or following showers of rain. The frequency of courtship behaviour increased to a maximum when the above factors were associated with a high tide.

When the rising tide in the evening covered the surrounding reef and sand banks, snakes frequently moved from the water to the land and vice versa. During such tides in summer months, males moved along the beach parallel to and often just within the water (Plate 9). Males detecting the point of exit of a female, presumably by smell, left the water and pursued the female. Hence the tracks left by emerging snakes were not evenly distributed along the shore but clumped together near the position of a female's emergence. During the pursuit males were observed to crawl onto the backs of the females. Females paid little attention to the males during courtship. During the period of pursuit and later in copulation there was no sign of male combat or displacement activity of unsuccessful males. Females showed no observable interest in male escorts which numbered as many as five on one occasion. If the persistence of the males disturbed the female, she returned to the water followed by the males. Often she returned to land a short distance along the beach a few minutes later.

Males followed the scent of the females so intensly that they ignored my presence and continued their pursuit over any article with which the female had been in contact. In such situations when males were interrupted by the researcher, there was no aggressive behaviour and upon release, they continued on their way. Receptive females were motionless when approached by the male and played no active part in copulation. Other males often joined and wrapped themselves around the copulating pair. In such situations it was difficult to identify the successful male.

The following account of courtship and copulation was made on Sausau Island, date = 8th January 1982, air temperature = 30°C. Observations commenced at 15:05 hrs.

15:05 Female (s-v length = 135 cm) emerged from the water behind the mangroves and moved to about one metre above the high water mark and stopped.

15:34 Male # 1 (s-v length = 91.5 cm) emerged from the water and followed the path of the female to where she lay motionless. He several complete courtships were documented on Sausau Island. The majority of successful matings took place in the early evenings either during or following showers of rain. The frequency of courtship behaviour increased to a maximum when the above factors were associated with a high tide.

When the rising tide in the evening covered the surrounding reef and sand banks, snakes frequently moved from the water to the land and vice versa. During such tides in summer months, males moved along the beach parallel to and often just within the water (Plate 9). Males detecting the point of exit of a female, presumably by smell, left the water and pursued the female. Hence the tracks left by emerging snakes were not evenly distributed along the shore but clumped together near the position of a female's emergence. During the pursuit males were observed to crawl onto the backs of the females. Females paid little attention to the males during courtship. During the period of pursuit and later in copulation there was no sign of male combat or displacement activity of unsuccessful males. Females showed no observable interest in male escorts which numbered as many as five on one occasion. If the persistence of the males disturbed the female, she returned to the water followed by the males. Often she returned to land a short distance along the beach a few minutes later.

Males followed the scent of the females so intensly that they ignored my presence and continued their pursuit over any article with which the female had been in contact. In such situations when males were interrupted by the researcher, there was no aggressive behaviour and upon release, they continued on their way. Receptive females were motionless when approached by the male and played no active part in copulation. Other males often joined and wrapped themselves around the copulating pair. In such situations it was difficult to identify the successful male.

The following account of courtship and copulation was made on Sausau Island, date = 8th January 1982, air temperature = 30°C. Observations commenced at 15:05 hrs.

15:05 Female (s-v length = 135 cm) emerged from the water behind the mangroves and moved to about one metre above the high water mark and stopped.

15:34 Male # 1 (s-v length = 91.5 cm) emerged from the water and followed the path of the female to where she lay motionless. He moved onto the back of the female and rested there in a zig-zag fashion for a while and then to her right side where he lay parallel to her.

15:40 Male # 1 started rhythmic spasms of his body which was pressed against that of the female. Ten contractions, with roughly equal periods of relaxation, took 41.6 seconds to complete (14.4 spasms per minute).

15:50 Male # 2 (s-v length = 74 cm) emerged from the water to join the pair and crawled onto the back of the female. The tail of Male # 1 was placed over the back of the female so that their cloacas were close together.

15:55 Male #3 (s-v length = 74.5 cm) emerged from the water and joined the others and crawled on the back of the female. Male # 2 was in a zig-zag position on the back of the female. The spasms of Male # 1 continued at the rate of 20.2 per minute.

16:03 Male # 4 (s-v length = 71 cm) emerged from the water and joined the others in the group. Insertion of Male # 1's left hemipenis into female. Spasms of Male # 1 were 23.6 per minute.

16:06 Male # 3 lay in a zig-zag fashion over the back of the female. Spasms of Male # 1 were 23.7 per minute.

16:11 Males # 2 and # 3 moved to the female's head and rubbed their mouths and lower jaw against her head and side. The female looked around occasionally but made little movement. Spasms of Male # 1 were 19.8 per minute.

16:13 Male # 1 removed hemipenis and spasms stopped.

16:16 The female moved off with Males # 2 and # 3 still on her back. At this point observations stopped and the specimens were collected for measuring.

Both sexes were observed to be "promiscuous" in their sexual activity. Individual males were recorded in courtship with several females during the visit to Sausau Island. Females were also recorded as being courted by different males throughout a twenty-four hour period and on successive days.

(ii) Female Reproductive Biology.

(a) Follicle Development and Ovulation

The ovarian follicles and oviducal eggs were grouped into six classes based on their maximum diameter and their stage of maturation according to Betz (1963) and Zug et al. (1979). The choice of size classes was determined by observations and measurements of the follicles and oviducal eggs of 68 specimens collected at various times throughout the year. The follicles formed five discrete groups, based on size, within the ovaries. Th sixth class comprised the oviducal eggs. Follicle diameters which had lower frequencies were taken to form the limits of a particular class. Table 11 presents the classes of follicles and oviducal eggs and the phase of maturation after Zug et al. (1979).

There was no seasonal shift in follicle size except for those in active vitellogenesis and maturation (Classes IV and V respectively). More follicles reached Class IV than developed into Class V and eventual ovulation.

Comparisons between the number of follicles in the left and right ovary and the number of oviducal eggs in the left and right oviduct revealed the following:

(1) There was no significant difference between the number of Class V follicles and the total number of oviducal eggs in the oviducts ($T = 0.26$, dof = 31, $P < 0.1$). All Class V follicles mature to oviducal eggs.

(2) There was no significant difference between the number of Class V follicles contained in the left and right oviducts ($T = 1.49$, dof = 44, $P < 0.1$). Reproductive output was shared evenly between left and right ovaries.

(3) There was a significant difference between the number of oviducal eggs contained in the left oviduct and that contained in the right ($T = 4.9$, dof = 18, $P < 0.005$). The right oviduct contained 111% more oviducal eggs than the left oviduct. This represented a considerable extra-uterine transfer. In a specimen (RA 140) which had recently ovulated, this transfer was evident. The left oviduct contained one less oviducal egg than corpora lutea in the left ovary. The right oviduct had one more oviducal egg than the number of corporea lutea in

the right ovary. The transfer had been from left to right.

Reciprocal extra-uterine transfers were not evident. Such transfers would be difficult to detect. Evidence for ova not reaching either oviduct was recorded for a single specimen (RA 141) which possessed eight ectopic eggs in the abdominal cavity. All were atretic and reduced in size.

The corpora lutea are short-lived after ovulation and in only a few cases were they detectable as small flaccid bodies after parturition. Dr. George Zug, Smithsonian Institution, verified these observations when, in 1981, he examined the dissected material from this study.

(b) Reproductive Cycle.

The results of the survey are summarised in Figure 7. The ovary weight index varied throughout the year. Minimum values were recorded in the winter months of June, July and August. This corresponded with the time of shortest photoperiod and coolest temperatures. Maximum values occurred in the summer months. This trend was evident also in the diameter of the largest follicle in the ovary of specimens collected throughout the year. The ovaries contained Class IV follicles during the winter months. These had grown to Class V follicles (> 15 mm) in October and were still present in March. Spermatozoa were found in the oviducts from October to April and females contained oviducal eggs from late October to April. Based on this evidence, Fijian female _L. colubrina_ were strongly seasonal in their reproductive cycle. These findings were supported by observations in the field. Mating activity was recorded from October to April.

(c) Size at Maturity.

The minimum size for a female carrying oviducal eggs was 98.5 cm. Measurements of the cloacal moulds indicated that females, smaller than 90 cm, were not capable of accepting the hemipenis of a mature male (Figure 8). Within the size range of 90 cm to 100 cm (s-v length), the length of the cloaca increased to that of a mature female. After 100 cm (s-v length), the length of the cloaca increased slightly with the s-v length of the female.

The regression equations for the three sections of the graph (Figure 8) are given below;

(i) [s-v length < 90 cm] $y = 0.008x + 0.003$, $r = 0.98$.

(ii) [s-v length 90 - 100 cm] $y = 0.014x - 0.015$, $r = 0.96$.

(iii) [s-v length > 100 cm] $y = 0.018x - 0.078$, $r = 0.84$.

where y is the length of the cloacal mould, x is the s-v length, and r is the correlation coefficient.

Variations in cloaca length were not seasonally related. Maturation commenced at 90 cm (s-v length) and continued until about 100 cm, when the first clutch of eggs was laid. The size of a female, at this first parturition, would be greater for those maturing in the winter months than for those reaching maturity in the summer months, because the former would have been at reproductive size for some months before mating took place.

(d) Clutch Size.

Within a clutch there was considerable variation in egg size. The lengths, widths and weights of the eggs in five clutches laid in captivity are given in Table 12. The eggs were white in colour and had soft parchment-like shells (Plate 10). They lacked adhesive properties, unlike those described by Mao and Chen (1980) for <u>L. semifasciata</u>. The contents were homogeneous throughout and lacked a discrete albumen and yolk. The mean clutch size was 6.0 (SE = 0.25, range 3 to 10, N = 49).

Figure 9 presents the relationship between maternal s-v length and the number of eggs in the clutch. The clutch sizes were obtained by either a direct count of eggs laid by females in captivity, or counting the number of oviducal eggs in the females dissected, or by palpation of females in the field to establish the number of oviducal eggs in the oviducts. Counts in the field were verified by the collection and dissection of a sample of females.

Larger females tended to have more eggs in a clutch than did smaller specimens. The relationship between s-v length and clutch size is expressed by the following the regression equation;

$$y = 0.1x - 5.03$$

where x is the s-v length in cm, y is the clutch size. The correlation coefficient (r) equals 0.47 and the sample size (N) equals 49.

(e) Reproductive Effort.

The reproductive effort of a species is the ratio of clutch weight to maternal body weight (C:B). To avoid errors associated with desiccation or absorption of water after laying, shelled oviducal eggs were used. Ten clutches of shelled oviducal eggs were weighed and divided by the weights of their respective maternal body weights. The mean C:B ratio is 0.175 (SE = 0.015, range = 0.124 to 0.26). The reproductive effort per egg (C:B/ clutch size) showed less variation (mean = 0.034, SE = 0.004, range = 0.018 to 0.065). The reproductive effort (C:B) showed little variation with s-v length or weight.

(f) Incubation and Hatching.

Early attempts to hatch the eggs were unsuccessful. As no eggs were found in the wild, the exact conditions for incubation were not known. Incubation trials which involved eggs placed in contact with sand moistened with fresh water and others with sea water, were equally unsuccessful. In December 1981, a captive female laid a clutch of seven eggs. These were carefully removed from the cage for incubation trials. Their upper surfaces were numbered with an alcohol-based marker pen to maintain orientation during handling. The eggs were measured, weighed and placed in a plastic bag with a light sprinkle of tap water. The bag was loosely sealed to prevent water loss and to exclude flies or other organisms that could have damaged the eggs. The bag was placed on a laboratory shelf where it would not be disturbed.

Eggs that became flaccid and turned black were removed in the early stages to prevent any possible contamination of those remaining. By the end of January 1982 only four eggs remained turgid and white. These were left to complete their incubation. In early March two eggs became flaccid and dehydrated. The remaining two appeared to increase their turgor. In early April 1982, the first of the eggs hatched followed five days later by the other (Plate 11).

Table 13 provides the s-v lengths, weights, incubation periods of each hatchling. Exit from the shell was facilitated by a well formed egg tooth on the premaxillary bone. In each case the shell had been slit lengthwise. The incubation periods of 121 and 126 days agreed with that of 137 days reported by Behler (1979) for eggs laid in

April by captive Fijian L. colubrina, in the Bronx Zoo, New York.

(iii) Male Reproductive Biology.

(a) Testicular Cycle.

Figure 10 presents the variation in testis weight index with the month of capture. The minimum values were obtained from specimens captured in April and May. The maximum value was obtained in October. The male sexual cycle was found to be synchronous with that of the female. During the winter months, males were sexually inactive. Sexual readiness, as determined by testis weight index, increased to a maximum in October and remained high throughout the summer before decreasing again in April.

(b) Description of Hemipenis.

Each hemipenis when everted was a single structure with a bulbous, bifid tip where it attained its maximum diameter (Plate 12). The organ comprised three parts. The proximal base of the hemipenis was smooth with a distal constriction beyond which a region of small spines rapidly gave way to larger spines. It was through this spinous region that the sulcus spermaticus was most obvious. The distal portion of the organ was covered with calyces whose edges were scalloped into small spines. In this calyculate area, the sulcus spermaticus divided and passed through the forked tip and spiralled back to terminate in an even more calyculate area on the tips. The morphology of the hemipenis, as described, agrees with the description given by Mao and Chen (1980) for Taiwanese specimens.

(c) Size at Maturity.

Table 14 presents the mean, standard error and range of hemipenis measurements of 33 male L. colubrina. These are presented graphically in Figure 11 (a - d) where the tip-to-tip distance, the maximum diameter, the length of the calyculate region and the length of the spinous region are plotted against the s-v length of the specimen. The adult size of the hemipenis was taken as the minimum of the 95%

confidence limits of the mean of each hemipenis parameter. At 70 cm s-v length, the males in the sample had reached sexual maturity, in that the hemipenis was of the dimensions of adult specimens and therefore, presumably were capable of copulation. Small males (s-v length = 60 cm) were found in courtship positions with females but these smaller specimens were not observed to be successful in copulation.

The weight of the testes was directly proportional to the body weight of the specimen (Figure 12). This relationship was shown by the following regression equation;

$$y = 0.01x - 0.28$$

where y was the weight of the testes (in grams) and x, the weight of the specimen (in grams). The correlation coefficient (r) was 0.78 and the sample size (N) was 36. There was a stronger correlation between the weight of body fat and the weight of the testes (Figure 13). The regression equation of

$$y = 0.1x + 0.51$$

was obtained where y represented the weight of the testes in grams and x equalled the weight of body fat also in grams. The correlation coefficient (r) was 0.87 and the sample size was 36. This demonstrated the importance of condition of the snake, in terms of body fat, in spermatogenesis and reproductive readiness.

D. DISCUSSION

(i) Courtship and Mating

Generalised descriptions of courtship and mating in snakes appear in most books on Herpetology e.g. Goin and Goin (1971) and Porter (1972). Shine, Grigg, Shine and Harlow (1981) provided a complete account of courtship and mating of the Australian elapid *Pseudechis porphyriacus*. A review of the literature revealed no documentation of courtship behaviour of *Laticauda*.

From the limited information available, *Laticauda colubrina* had a number of behavioural traits in common with other snake species in general (Porter, 1972). During courtship, males rubbed their chin on the female's head, neck and back. The rhythmical contractions of the male, during courtship and copulation, had been recorded also, for other snake species. The contractions, observed in the present study, could not be described as "caudocephalic waves" as reported for *Storeria* and *Thamnophis* by Porter (1972). The contractions of male *L. colubrina* did not originate in the caudal region and progress towards the anterior but involved the entire body in a simultaneous spasm.

Male to male combat, as reported by Shine *et al.* (1981) for *P. porphyriacus*, was not observed in *L. colubrina* in spite of there having been numerous males present with a female. Female involvement in courtship and copulation was minimal. Throughout the entire course of activities, females remained motionless apart from slight movements of the head.

(ii) Female Reproductive Cycle

(a) Ovulation

Because some females contained abundant sperm in their oviducts, yet their largest follicle was less than 15 mm (active vitellogenesis - Class IV follicles), it appeared that copulation preceded ovulation. Unless these females mated again, the spermatozoa would have to be retained in the oviducts for some weeks until ovulation tool place. However, with an abundance of males in the population and *L. colubrina* being gregarious, the need for specialised sperm storage organs as reported for *Thamnophis* (Fox 1956 in Porter 1972) seems unlikely.

The disparity between the number of corpora lutea in the ovary of one side and the number of oviducal eggs on the same side was first reported for snakes by Betz (1963) and described as extra-uterine migration after Legler (1958) described the process in turtles. Shine (1977b) recorded extra-uterine transfer in three species of Australian elapid. In each species the most common direction of movement of the oocytes was from left to right oviduct. Voris and Jayne (1979) reported the right ovary as more productive than the left and the right oviduct contained more oviducal eggs than did the left oviduct of *Enhydrina schistosa*. Betz (1963) reported similar findings for *Natrix rhombifera*. Bergman (1943) recorded the right oviduct as containing usually more embryos for the six species of viviparous sea snake from Java.

The trend within the snakes to utilise the right oviduct by, either producing more ova in the right ovary or, producing an equal number in each ovary and transferring some of the products of the left ovary to the right oviduct, remains poorly understood. Shine (1977b) argued this transfer to the right oviduct to be a simple consequence of space limitations within the body of the females.

(b) Seasonality

Fitch (1970) assumed aseasonal reproduction to be normal for subtropical and tropical snakes. Neill (1962 in Porter 1972) found that in British Honduras snakes representing 11 genera and four families, appeared to have well defined breeding cycles and concluded that reproduction was curtailed, as in non-tropical areas by minimal temperatures. Saint Girons (1982) recorded additional exceptions to the aseasonality of reproduction of tropical snakes. Several species of sea snake were recorded as being seasonal in their reproduction; Lapemis hardwickii, Thalassophis anomalus, Enhydrina schistosa, Hydrophis fasciatus, H. brooki, H. cyanocinctus (Bergman, 1943; Voris and Jayne, 1979; Lemen and Voris, 1981). Smedley (1931b) reported seasonal reproduction for L. colubrina in Singapore. Laticauda colubrina was thought to be seasonal in New Caledonia (Saint Girons, 1964; Laboute and Magnier, 1979) although little reproductive data were presented and reports were anecdotal. Gorman et al. (1981) reported L. colubrina as aseasonally reproductive in the Philippines, inspite of few adult females in their sample.

The present study indicated L. colubrina was strongly seasonal in Fiji. Courtship and mating were confined to the summer months, i.e. October to April. Egg laying also occurred during this period. During the winter months, May to September, ovarian follicles were, without exception, small (< 15 mm) in the females sampled. In males, the testes were proportionally smaller during winter months and there was no courtship activity observed in the wild populations.

There was no anatomical evidence to suggest that more than one clutch was laid by a female during the breeding season as suggested by Pernetta (1977). Therefore, L. colubrina displayed a monoestrus, seasonal mode of reproduction. That is in agreement with the scheme proposed by Saint Girons (1982).

(c) Female Size at Maturity

Recent literature provided little information on the size of female L. colubrina at sexual maturity. Saint Girons (1964) suggested that copulation took place before the females reach two years of age, but added that the first oestrus may occur without vitellogenesis. According to his data, this placed sexual maturity in the 65 to 80 cm class size. Pernetta (1977) described female specimens with a total length in excess of 93 cm. He did not comment on size at maturity, but did mention that sexual dimorphism in size was apparent in a female whose total length was 50.5 mm and for that of male of 40.3 mm. The units are in question for I assume centimetres are what were intended. Gorman et al. (1981) restricted their studies to females with a s-v length in excess of 101 cm. Pimento (1972) reported a single female L. colubrina with seven oviducal eggs. The length was given as 990 mm without further reference. The present study set the size of females at sexual maturity at between 90 and 100 cm. The selection of this size class was based on the dimensions of the cloaca and the smallest specimen (s-v length = 98.5 cm) with oviducal eggs.

(d) Clutch Size

From observations on six captive females, Smedley (1931b) reported the average clutch size of L. colubrina was six. Saint Girons (1964) estimated the clutch size of L. colubrina as 15 and calculated age class mortality and recruitment accordingly. Gorman et al. (1981) suggested the clutch size was between 4 and 19. They also suggested the existence of a clutch size to body size relationship for Philippine specimens. As noted above, Pimento (1972) reported a single clutch of seven. Pernetta (1977) recorded the average clutch size as 6.7 for Fijian specimens. Guinea (1981), and the present survey, placed the maximum clutch size at 10 with an average of 6 (SE = 0.25) eggs per clutch for L. colubrina in Fiji. A weak relationship (r = 0.47) existed between clutch size and s-v length. This was not so pronounced as similar relationships reported for species of terrestrial elapid (Shine, 1980 a and b), colubrid (Zug, et al., 1979) and hydrophiid (Lemen and Voris, 1981).

(e) Reproductive Effort

An important aspect of the reproductive biology of sea snakes is the relationship that exists among the female weight, clutch size and birth weight and reproductive effort. The reproductive effort (ratio of clutch weight to maternal body weight C:B) showed little variation when compared with those given for five species of viviparous sea snake by Lemen and Voris (1981 Table 3). Shine (1977b) stated that the general pattern in reptiles was for the reproductive effort (C:B) to remain relatively constant with age. Older specimens tended to devote more of their available energy to reproduction than did younger ones because the food intake per gram body weight was lower in larger animals.

Differences in reproductive strategies involved the extent to which available space was utilised and whether the species produced many small young or a few large offspring. Enhydrina schistosa was an example of the former producing on average 18 young with an average birth weight of 11 grams (Lemen and Voris 1981). L. colubrina produced an average clutch size of six with an average egg weight per clutch of 22.7 grams (Guinea 1981). The weights of the two young hatched in captivity were 23.8 and 17.3 grams yet, at the time of hatching, 35% and 50% of the egg weight remained after the hatchlings had emerged (Table 12). This material (waste, water and shell) represented an amount of material that would have either been supplied by the mother or absorbed from the environment. Unlike the truly viviparous species, Pseudechis porphyriacus which showed true placentation and transfer of nutrients (Shine 1977b), L. colubrina provided all the nutrients required for embryogenesis, excluding oxygen and some water, to the eggs at parturition. Those nutrients not utilised by the embryo were lost to the mother. Therefore, the reproductive effort of oviparous species is likely to be higher than viviparous species. This was found not to be the case. Shine (1977b) presented the C:B ratios of four, Australian, viviparous, elapid species. In each species, (Austrelaps superbus, 0.28; Notechis scutatus, 0.42; Pseudechis porphyriacus, 0.22; Unechis gouldii, 0.58) the C:B ratio was greater than the average for L. colubrina (0.175). Of the ten species of viviparous sea snake reported by Lemen and Voris (1981), each had a C:B ratio greater than that calculated for L. colubrina in this study. These ranged from 0.236 (Aipysurus granulatus) to 0.389 (Enhydrina schistosa). The explanation of such a small C:B ratio, and therefore low reproductive effort for L. colubrina remains obscure.

(f) Incubation and Hatching

Information on the incubation period of L. colubrina was limited to the editor's comment in Behler (1979) which gave the incubation period as 137 days and to an estimate of 13 weeks by Guinea (1981). Saint Girons (1964) restricted hatchling size to less than 45 cm. In Fiji, juveniles of this size were found in the study areas in February. These were thought to be the offspring from the previous breeding season whose embryogenesis had been retarded by the cooler temperatures during the winter months (see chapter 7 on Growth). Porter (1972) reported that an increase in ambient temperature of 1°C can shorten the gestation period by four and one half days. In Fiji, the monthly mean temperature was 4°C higher in the summer months than during the winter (see figure 3). Eggs laid in December hatched 18 weeks later in April. Those laid in April hatched possibly in September, i.e. 22 weeks later.

Guinea (1981) reported that the eggs of L. colubrina had the ability to gain weight by freshwater absorption in the first 24 hours after laying. They became flaccid when placed in sea water. From these observations, it was concluded that the shell provided little resistance to the movement of water molecules. Initial investigations in the laboratory indicate that the shell also allowed oxygen to diffuse freely into the egg. The eggs behaved in a similar manner to many other reptilian eggs with parchment-like shells e.g sea turtles and iguanas. Successful hatching trials involved the eggs being kept moist with the majority of the surface area in contact with air. The eggs of L. colubrina are likely to be laid in crevices in rock where they are protected from desiccation and in contact with air and freshwater. Such places were numerous in the study areas but as previously mentioned, were so narrow as to exclude human entry.

Oviparity and ovoviviparity in L. colubrina were discussed by Smith (1930) and Smedley (1931 a and b). None of the eggs laid in captivity during this study showed signs of advanced embryonic development. These may have been, as argued by Smith (1930), laid prematurely as a consequence of captivity. The eggs observed in the present study were laid as a single egg per day by some specimens and as a clutch, within a few hours by others. The rate at which the eggs were laid, was considered of little importance in the present study.

(iii) Male Reproductive Cycle

(a) Seasonality

Gorman _et al._ (1981) reported aseasonal breeding in _L. colubrina_ as mentioned before. On close examination of their data for males, low plasma testosterone levels were found in specimens captured during the winter months in the Philippines (August to March). The higher values did occur in the summer months but were not reproducible from year to year. However, they stated that there was no correlation between plasma testosterone and testes size (weight).

The present study revealed that males had a higher testes weight index during the spring and summer months (September to February) in Fiji. The remainder of the year was characterised by relatively low testes weight indices. Females were found with spermatozoa in the oviducts from October to April. Male _L. colubrina_ in Fiji, displayed 'prenuptial' and 'mixed' spermatogenesis according to the scheme proposed by Saint Girons (1982).

(b) Male Size at Maturity

Based on histological studies, Saint Girons (1964) reported that males larger than 50 cm were mature. Results from the present study suggested that this figure was too small. Measurements of the hemipenis indicated that adult size was attained at about 70 cm (s-v length). The smallest male specimen used by Gorman _et al._ (1981) was 77.5 cm (s-v length).

Shine (1980c) commented that species in which there was no male combat in courtship usually had pronounced sexual dimorphism in favour of female superiority in size. He continued that in _Cacophis_ not only did the females grow larger than males but tended to mature at larger sizes and at later ages (Shine 1980c). In _L. colubrina_, males were smaller, did not display male combat, and matured earlier than females (see Chapter 7, Growth).

6. FEEDING BIOLOGY

A. INTRODUCTION

Several authors reported the diet of L. colubrina as exclusively eels (Saint Girons, 1964; Pernetta, 1977; Guinea, 1981). Voris (1972) recorded eels (Moringuidae and Muraenidae) but also lists non-eel prey (Synodontidae, Synodus and Pomacentridae, Glyphidon sp. and Glyphisodon sp.) from Palau Is. McCoy (1980) reported L. colubrina feeding on fish (Gobiodon sp.) and lizards in the Solomon Islands. Glodek and Voris (1982) recorded only eels (Anguilliformes) from the stomachs of L. colubrina from the Straits of Malacca. In order to detect any deviation from a strict eel diet in Fiji, the stomach contents of L. colubrina specimens dissected for studies on reproduction (Chapter 5) were examined and identified where possible.

B. METHODS

Information on stomach contents was collected whenever possible. This involved the removal of the stomach contents from specimens dissected for investigations into the reproductive biology (see Chapter 5). Stomach contents which showed little digestion were preserved in 10% formalin and used as reference for other material in poorer condition.

A sample of individuals caught in the field, had their stomach contents removed by gently forcing the contents of the stomach and oesophagus out through the mouth. The snake, when released, showed no adverse effects from the treatment. Stomach contents, collected from the field, were identified, weighed, measured and photographed. The eel species were identified using the reference collection of the Institute of Marine Resources at USP and Carcasson (1977).

Individual L. colubrina were followed underwater with SCUBA equipment. Such underwater observations were conducted around Mabualau Island and in Laucala Bay and Namuka Harbour. Dives to areas of Laucala Bay and Namuka Harbour, where L. colubrina were sighted during the day, were repeated at night to investigate nocturnal feeding activity.

C. RESULTS AND OBSERVATIONS

In Fiji, the prey species belonged to two families exclusively, namely Muraenesocidae (Conger Eels) and Muraenidae (Moray Eels). Table 15 lists the species of eel removed from the stomachs of L. colubrina from S.E. Viti Levu. Eels of considerable size were removed from the stomachs of females. In one case the stomach contents represented 69% of the snake weight. The relative size of snake to eel was demonstrated by Plate 13 which showed a radiograph of an adult female L. colubrina with an eel (Gymnothorax sp) positioned head first in the stomach: the remainder of the eel occupied the oesophagus. It was doubtful that the entire eel would have been digested. In such circumstances the rate of putréfaction of the eel would determine how much was digested before the remainder was regurgitated. Partly digested eel remains were commonly found around Namuka and Vuiva Islands. Presumably, these remains were regurgitated voluntarily.

The positions of female snakes with obvious engorged stomachs were noted at Namuka and Vuiva Islands. The islands were revisited seven days later to test if the snakes had remained in the area to digest their prey. The females in each case were neither in the same position nor even on the island. No snake was found to be in the same position after a seven day period.

Of the snakes that had the stomach contents removed, the prey had been swallowed head first in 82% of the cases. The elongate form of the eels and the snakes excluded the possibility that the eel may have changed orientation after ingestion. The species taken by males were the same as, in several cases, but smaller than those taken by the females. This indicated, as suggested by Pernetta (1977), that males fed in shallower water than did females.

Underwater observations on L. colubrina around Nabualau Island and in Laucala Bay did not include witnessing the capture of a prey item. Individuals were observed moving between coral boulders and investigating hollows and crevices. SCUBA dives in Laucala Bay and Namuka harbour at night failed to reveal any L. colubrina activity on the reef crest or in adjacent deep water.

During trips to Sausau Island in April and July 1981, and January 1982, the presence of noticeable stomach contents was used as part of the description of specimens captured. In spite of the fluctuations in the numbers of individuals using Sausau Island during the year the proportion of female L. colubrina with noticeable stomach contents remained at about 10% (Chi Square = 0.16, dof = 2, $P < 0.05$). As males fed on smaller eels, the presence of a full stomach was not as noticeable and a similar comparison for this sex could not be made.

D. DISCUSSION

Voris (1972) concluded that the prey of Laticauda was narrowly restricted to bottom dwelling forms associated with rock and coral outcrops. The absence of non-eel fish as prey items in Fiji, could have indicated an abundance of eels or possibly, a local preference for eels. Bottom dwellers, including Synodontidae, were present in Fiji as were the reef dwelling Sergeant-majors (Glyphisodon), but they were not recorded amongst the stomach contents of sea snakes. There was no indication that L. colubrina fed on terrestrial vertebrates e.g. lizards, although these too, were common on all of the islands investigated.

It was assumed that L. colubrina fed during the day and located prey by sight. Evidence for this came from observations made when a banded snake eel Myrichthys colubrinus swam through a group of L. colubrina in clear water at the edge of the mangroves on Sausau Island. Neither the snakes nor the eel seemed interested in the other. The colouration of the eel may have been responsible for the deception. An eel of the same species and a L. colubrina were kept in the same aquarium for several days without incident. Hydrophis melanocephalus struck without delay at the same eel when it was placed in an aquarium with them.

Several prey species of eel were observed sheltering in crevices in coral and rubble on the reef crest. Presumably, their captured by L. colubrina takes place in similar situations, although no captures were observed. Johannes (1981) reported an interesting piece of folk-lore from Palau, which concerned L. colubrina. It went as follows; "They [the Palauans] noticed that sometimes when the 'mengerenger' [L. colubrina] withdrew its head from a hole where it had been searching for food, small fish would come gyrating out in obvious distress and swim convulsively for a few seconds before being caught and swallowed by the snake. This led to the belief that the 'mengerenger' "breathes poison" into the water." (Johannes, (1981 p137). This description of the fish having been trapped in a hole by the snake, bitten and envenomated, and left to succumb before being eaten, was similar to that given for L. laticaudata feeding in captivity (Klemmer, 1967) and for L. semifasciata feeding, also, in captivity (Pickwell, 1972). Dunson (1975) reported that Laticauda used coils of its body to immobilize a fish before it was seized and swallowed. Further research into the feeding behaviour of L. colubrina in the wild, would prove worth-while.

Saint Girons (1964) postulated that in New Caledonian populations, some snakes remained on land to digest their prey for at least two weeks and, possibly, for more than a month during winter. This seemed unlikely to occur in Fiji for no specimen with obvious stomach contents was sighted in the same position or even found on the island after a period of seven days.

Considerable time would be required to digest large eels. McCosker (1975) described feeding experiments which showed that an adult Hydrophis melanocephalus required 2 to 3 days to digest a juvenile moray eel (185 mm) at 25°C. Klemmer (1967) fed his captive L. laticaudata which were kept at 24°C, "about three eels (medium-sized Anguilla) every 2 months" There exists a need for more research into this aspect of the feeding biology of sea snakes.

7. GROWTH

A. INTRODUCTION

Information on growth and age at maturity of sea snakes was limited to estimates of growth for L. colubrina by Saint Girons (1964) and that of Voris and Jayne (1979) who completed a more detailed investigation into the growth of Enhydrina schistosa in Malaysia. As individuals were not tagged in the present survey, a static estimation of growth for juveniles and subadults was obtained.

B. METHODS

Two methods were employed to obtain growth rates for juvenile L. colubrina. Firstly, observations and measurements were made at an interval of six months, on a group of juveniles inhabiting two rocky outcrops, one and one half kilometres North West of Sausau Island. Secondly, as many small (non-adult) individuals as possible were caught in the study areas of S.E. Viti Levu and measured to the nearest 0.5 cm using a fibreglass tape. From these latter data a body size - month of capture matrix was constructed for each sex.

C. RESULTS AND OBSERVATIONS

(i) Growth Rates

An estimate of growth rate came from observations on an aggregation of juveniles using rocky outcrops North West of Sausau Island. In July 1981, 31 juveniles were caught on the rocks during a falling tide. A sample of six specimens were measured (mean s-v length = 39.1 cm, s.e. = 1.39, range = 35 to 43.5 cm). The remaining specimens were of similar size. During a high tide in January 1982, 23 specimens were caught on the same rocks and measured (mean s-v length = 62.8 cm, s.e. = 0.87, range = 52 to 73 cm). The increase in mean s-v length by 23.7 cm in 26 weeks gave an implied growth rate of 0.91 cm/week.

Using the second method, the body size - month matrices for males and females were constructed for the population of S.E. Viti Levu. The matrices (Figure 14 (a) and (b)) comprised the number of individuals of each s-v length class size, caught in a month. Young of the year (s-v length < 45 cm (Saint Girons, 1964) were found from February to December. The seven month reproductive season (October to April) and the long incubation period (four to possibly five months) meant that young were found during most months. However, the smallest individuals (s-v length of about 30 cm) were found from April to October.

(ii) Age at Sexual Maturity

The data may be interpreted in two ways. Assuming a constant growth rate in the first year of life, the implied growth rate of 0.91 cm/week meant that a male snake could grow from hatching (s-v length about 30 cm) to sexual maturity (s-v length about 70 cm) in 36.4 weeks (nine months). A male that hatched in February could be engaged in reproduction the following November. A female could take just over 59 weeks (about 15 months) to reach sexual maturity. Should sexual maturity coincide with the mating season, the first clutch of eggs could be produced within 18 months of birth.

These ages appeared too low for adulthood when compared with those suggested by Saint Girons (1964) and Voris and Jayne (1979) for E. schistosa. A more reliable estimate of age at sexual maturity was obtained when the data for non-adult specimens shown in Figure 14 (a) and (b) were placed in sequence based on s-v length and month, irrespective of the year of capture (Figure 15 (a) and (b). The growth curve, thus produced, was similar in shape to that presented for Enhydrina schistosa by Voris and Jayne (1979). From Figure 15 (a), males reached adult size (70 cm) about 15 months after their birth. Females, although they had a similar growth pattern to males for the first year of their life, reached adult size 26 months after their birth.

D. DISCUSSION

(i) Growth Rates

Voris and Jayne (1979) reported an average growth rate of 0.7 cm/week for Malaysian _Enhydrina schistosa_ during their first year. Growth rates within that period were recorded as 0.84 and 2.3 cm/week. Growth rate decreased as the snakes approached adult size. _L. colubrina_ in the present study, appeared to follow a similar trend. Male and female growth rates were equal in the first year, after which the males reached maturity and the females continued through a subadult year before they were of adult size. During the subadult year, the females doubled their body weight and increased their s-v length by 25% to 100 cm.

(ii) Age at Sexual Maturity

Shine (1978; 1980 (a) and (b)) gave the age at sexual maturity for several species of Australian elapids. From his findings, some females mated at 12 months of age (_Unechis gouldii_, _Hemiaspis daemelii_ and _H. signata_) others at about 20 months (_Demansia psammophis_, _Cacophis krefftii_) or 24 months (_Austrelaps superbus_, _Notechis scutatus_) or 31 or 32 months (_Pseudechis porphyriacus_, _Cacophis harriettae_ and _C. squamulosus_). In most species males reached maturity after 12 months.

Voris and Jayne (1979) estimated _Enhydrina schistosa_ males and females reached maturity at 18 months of age. Male _L. colubrina_ in New Caledonia matured at 18 months and females at 30 months (Saint Girons, 1964). Saint Girons assumed that most hatching took place in January instead of April, as indicated in this study. I assumed that the juvenile specimens reported in Saint Girons (1964), were younger than he estimated. When this difference of three or four months was taken into consideration, the predicted ages from the growth curves (Figure 15 a and b), of 15 months for males and 26 months for females, and those assumed by Saint Girons (1964), were in close agreement. The rapid growth and early age of sexual maturity of _L. colubrina_ are probably assisted by Fiji having a warm climate and an abundance of food species for juvenile snakes.

B. POPULATION STUDIES

A. INTRODUCTION

Saint Girons (1964) conducted mark and recapture studies on populations of L. colubrina on Petit Taenia and Signal Islands, New Caledonia. Within the present study, investigations were conducted to estimate the size and seasonal fluctuations of the population of L. colubrina which inhabited Sausau Island. The island was visited on four occasions. The initial visit was in February 1981 and lasted for only two hours. In April (21 - 24) the island was visited for four days during which the short-term mark and recapture programme was started. Again in July (9 - 12) the island was visited and mark and recapture studies were continued. During the breeding season, January 5 - 12, 1982, the island was monitored for the fourth time. The aims of this investigation were to estimate the number of L. colubrina present in the population on Sausau Island at several times of the year, to document seasonal changes in the population structure, and to identify the preferred habitats.

B. MATERIALS AND METHODS

Monel metal tags were used in a series of trials on female specimens kept in captivity at USP. The animals were sedated with "Ketalar"* (Ketamine hydrochloride; 0.22 ml per kg body weight, Burton, 1978). A tag was secured with pliers, through the dorsal segment of the tail of each snake. The tags did not stay in place and subsequently moved through the flesh of the tail. Eventually, all tags were dislodged amongst the rocks in the aquaria. This method of tagging was slow, and required the animal to be restrained during marking. The slowness and the trauma associated with tagging large numbers of specimens, plus being unsuccessful during trials, made this method unsuitable for this study. As the snakes on Sausau Is. were to be disturbed as little as possible during the survey, an alternative method was sought.

By the selection of a number of natural, individual markings and by the application paint to snakes as they were caught, a short-term mark and recapture programme was conducted during each visit to Sausau

Island. This enabled snakes to be marked while causing little disturbance to their behaviour. Snakes resting on shore, usually, neither returned immediately to the sea, nor changed their behaviour, after being caught. The marking procedure went as follows:

When an animal was sighted notes were made regarding its sex, number of prefrontal scales, number of black bands, the colour of the tip of the tail and the position of any scars. Notes were made on the colour of the eye scales; milky or white eyes indicated the snake was going to slough its skin in the near future. Also, the presence of ticks, or any aberration in banding pattern, infections or unusual pigmentation was recorded. The date, time and locality on the island were recorded for each observation. The snake was then sprayed with paint (British Paints Quick Dry Enamel) to form a five centimetre wide band across the body. Four colours of aerosol paint were used. All snakes caught in a twenty-four hour period were sprayed with the same colour. The initial marking was on the tail with subsequent recaptures being sprayed on the body anterior to the previous colour. This proceeded until all four colours had been used and then the colours were used in the same order, but were applied behind the head and progressed with subsequent recaptures towards the posterior. The pattern of colours and their positions indicated not only how many times a snake was caught, but also on which day or days.

This procedure enabled most snakes to be marked without disturbance. Most sleeping individuals did not awaken during the marking operation. The paint adhered quickly to wet and dry scales so that individuals just leaving or entering the water were marked successfully.

C. RESULTS AND OBSERVATIONS

(i) Habitat Descriptions

Figure 16 shows the habitat of the study region on Sausau Island. The island was divided into nine areas as listed below:

1. A ridge with an estimated height of 15 metres runs east-west forming the maximum diameter of the island. It is made up of volcanic tuff which is weathered in places to produce a thin soil which supports grass and low shrubs and an intermittent covering of

trees including _Casuarina_ spp. and _Pandanus_ spp.. It is distinguished from neighbouring areas in that to get to it, the snakes have to climb either a scree slope or a near-vertical rock face.

2. A region of tall grass is at the western base of Area 1 and consists of sand covered with grass and low shrubs with a stand of coconut palms to the west. The camp site, which bordered the mangroves and the beach, was located at the western end of this grassy area.
3. These mangroves stand at the head of a noticeable drainage system which fills quickly with the flood tide and provides an aquatic approach to the island from the western areas of Sausau Reef.
4. This stand of mangroves along the northern side of the island is inundated during the period of high water only. The mangroves give way on the land-ward side to a small stand of trees which provides a shaded corridor to the elevated ground of Area 1.
5. The southern mangroves are the most extensive on the island and accessible by sea at half-tide. The relatively narrow reef flat ensures that deep water is close at hand throughout most of the tidal cycle.
6. The prominent sandspit on the western end of the island forms a sandy beach between Area 2 and Area 5.
7. The rocks of this area face the prevailing wind and swell. Aquatic access is restricted to high tide only. This area is backed by the vertical rock face of Area 1.
8. The reef flat is extensive and covers an area of 23 km in length and up to 5 km in width. Several isolated mangroves grow over the reef flat to the north of the island. The reef flat is broken in many places by deep pools that retain water at low tide.
9. The region below the Low Water Mark (L.W.M.) makes up the ninth area. The water is not particularly deep close to the island. A depth of less than 10 metres was recorded 50 metres sea-ward of the L.W.M..

(ii) Mark and Recaptures

During the four visits to Sausau Island, a total of 1244 records were made on approximately 900 individuals. The method of marking did not allow individuals to be recognized on subsequent visits because the paint was shed with the next slough, as was observed on three occasions. The number of snakes observed on each visit exceeded one hundred. In April 1981 and January 1982 about 100 L. colubrina were captured each day. The distribution of the snakes on the island varied with the season. In July, the majority of animals were captured in Area 2 and the neighbouring mangrove patch, Area 3. The mangrove, Area 5, was heavily populated in April and January. Courting groups were found in this area (5) on both occasions. No courtship was recorded in July. Table 16 shows the distribution of the sightings of L. colubrina during the visits to Sausau Island in 1981 and 1982. Few juveniles were recorded except for a collection of individuals caught on two rocks on the reef flat (Area 8) 1.5 km North West of the island (see Chapter 7).

(iii) Sex Ratios

During the brief visit to the island in February 1981, The majority of the snakes were in two Areas (2 and 5). Males outnumbered females in Area 2 (2.4 : 1; M : F). In Area 5, females were slightly more numerous than males (1.1 : 1; F : M).

The longer visit in April revealed Areas 2 and 5 to be the most populated areas of the island. Males were slightly more numerous but the ratios of males to females were not significantly different from 1 : 1 (Chi Square = 0.11, dof = 1, $P < 0.75$).

In July, the snakes were found further inland as was indicated by animals being caught in Area 1. In Area 2, males and females were present in approximately equal numbers. Area 3 had more snakes than previously reported. Very few snakes were found in Area 5.

In January 1982, Areas 2 and 5 were again the most populated habitats on the island. Males outnumbered females (1.9 : 1 and 1.5 : 1; M : F, respectively). Fewer snakes were found inland in Area 1.

Analysis of data using Chi Square procedures and Yates correction for continuity (Zar, 1974) revealed a significant difference between the numbers of males and females found in Areas 2 and 5 in

February 1981 (Chi Square = 5.4, dof = 1, $P < 0.025$). However, there was no significant difference between the numbers of males and females using Areas 2 and 5 for each of the other months, April, July and January (maximum Chi Square = 1.1, dof = 1, $P < 0.5$).

When the entire number of L. colubrina recorded from Sausau Island during the four visits (Table 16) were analysed, the sex ratio did not differ significantly from 1 : 1 (paired-sample t test; t = 0.73, dof = 6, $P < 0.1$).

(iv) Population Size

The mark and recapture study was designed to produce an estimate of the population using the 'Petersen estimate' outlined by Caughley (1977) in which he reminded us that to produce an estimate with an acceptable error of 10%, 55 marked individuals had to be recaptured from an initial sample of 100 marked animals. As there was no previous estimate of this population on Sausau, and because the only previous study of this nature on L. colubrina produced large standard errors (Saint Girons, 1964), marking was conducted each day during the study.

Data for the 'Petersen estimate' came from the individuals marked during the first twenty-four hours and recaptured during the last twenty-four hours of each visit. Moribund individuals were deleted from the data. The modification to the 'Petersen estimate' suggested by Bailey (in Caughley, 1977) for direct sampling was used because the number of recaptures were well below those recommended above for a 10% error. Three individuals from a group of 66 which were marked in the first 24 hrs, were recaptured in a sample of 31 in the last 24 hrs of the visit in April. The 'Petersen estimate', with standard error, was calculated as 528 ± 221 i.e. 307 to 749. The estimate for July was 1159 ± 658 (501 to 1817). January's estimate was 3200 ± 1824 (1376 to 5024).

Data obtained from marking individuals each day, with subsequent recaptures on several days, were used to estimate the size of the population using 'Schumacher's method' (Caughley 1977). The Schumacher estimate of the population on Sausau in April was 913 (95% confidence limits = 309 to 956). The estimate for July was 1116 (95% confidence limits = 715 to 2535). January's estimate was 1584 (95% confidence limits = 1055 to 3168).

These methods were not free from uncertainties, among which included the catchability of L. colubrina. Caughley (1977 p135) referred to animals in general, when he stated "Unequal catchability, whatever the cause, is more the rule than the exception.". Caughley (1977 p136) demonstrated the test for equal catchability described by Orians and Leslie (1958). This test when it was applied to the data from Sausau Island, revealed unequal catchability for April ($P < 0.05$) and July ($P < 0.001$). The data for January indicated equal catchability ($P < 0.975$). As the 'Petersen estimate' and 'Schumacher's method' required equal catchability of the population to be effective, a third method of estimating the population was sought.

Caughley (1977 pp 152 -157) presented details of the 'frequency of capture models' which may be used to estimate the size of a population. Inherent in each model is the facility for estimating the catchability of the population. The analyses of a population by 'frequency of capture models' involves knowing the number of individuals caught once, twice, three times and so on, over several capture periods. These data form a zero-truncated frequency distribution of captures. The analysis attempts to estimate the frequency of the zero-class (those that were never caught) from the shape of the truncated distribution. The population is estimated by the addition of those individuals that were caught once, to those that were never caught (zero-class).

Zero-truncated Poisson, negative binomial and geometric frequency distributions were employed in the present study. The Poisson method assumed that the catchability was constant, whereas the negative binomial and geometric methods allowed for unequal catchability. A BASIC version of Caughley's (1977 p 216) FORTRAN programme for calculating the size of the population using the capture frequencies fitted to zero-truncated Poisson, negative binomial and geometric distributions appears in the Appendix.

The numbers of individuals captured once, twice, three times etc. during each visit to Sausau Island, were used to calculate three estimates of the size of the population for that time of the year. These are based on; (a) a Poisson distribution (equal probability of capture), (b) a negative binomial distribution (unequal catchability), (c) a geometric distribution (unequal catchability).

Chi Square analysis was used to test the goodness of fit of the data to each of these three distributions. The lowest value of Chi

Square indicated the best estimate of the population size. The estimates produced by the above three distributions for Sausau Island during April, July and January are shown in Table 17 (a, b and c) respectively. The population of L. colubrina on Sausau Island in April was estimated as 1075 (geometric distribution; Chi Square = 0.43, dof = 2, $P < 0.75$). In July, it was estimated as 1106 (geometric distribution; Chi Square = 0.58, dof = 2, $P = 0.75$). In January, the estimate was 1398 (Poisson distribution; Chi Square = 0.51, dof = 3, $P < 0.95$).

D. DISCUSSION

Saint Girons (1964) reported that the distribution of L. colubrina on the islands in New Caledonia was different for each of his visits. A similar pattern was shown by the distribution of L. colubrina on Sausau Island during the summer and winter months. In January, Areas 2 (grass and low shrubs) and 5 (mangroves on the southern side) were heavily populated. Areas 2 and 3 (northern mangroves) contained the largest number of individuals during the winter months. Apart from differences in aspect and slight variations in temperature that existed between areas, no satisfactory explanation was evident for this seasonal preference for different areas on the island.

Similar observations were made on Mabualau Island where during the winter months snakes were found in the interior of the island. Whereas in the summer months they were found along the shoreline on the lee-ward side of the island.

(i) Sex Ratios

Bergman (1943) reported that female sea snakes were more numerous than were males in two species, Thalassophis anomalus (2 : 1; F : M) and Enhydrina schistosa (4 : 3; F : M), from Java. Another four species had sex ratios of 1 : 1. Saint Girons (1964) reported that male L. colubrina were more numerous than females and made up 61.5% of the entire population. Males comprised 55.7% of juvenile snakes. The lack of a one-to-one sex ratio may have been due to a higher female mortality, as suggested by Klauber (1936) for certain crotalids, but Saint Girons (1964) suggested as an alternative, that female L.

colubrina spent a longer time at sea than did males, thereby reducing their relative abundance in the land populations and increasing their mortality through predation by marine animals. Voris and Jayne (1979) reported equal numbers of each sex for E. schistosa throughout most of the year in Malaysia. However, in their March sample, males outnumbered females by two to one.

The ratio of males to females on Sausau Island was not significantly different from 1 : 1 ($P < 0.1$), when all sightings from each visit were tested. However within areas differences did occur. Saint Girons (1964) with reference to his research on terrestrial snakes, reiterated that for adults, the sex ratio varied with the time and place of capture. This comment was also applicable to the studies on Sausau Island because within an area, males were caught often in different locations to females. Of the 37 males recorded from Area 2 (February 1981), 14 were caught in coconut trees. Only one female was recorded from the low axils (less than 2 m) of these trees. Males were caught rarely amongst the clumps of tall grass in Area 2 where resting females were observed.

The ratio of males to females varied also with season and locality on the islands of S.E. Viti Levu. The ship's boiler near Namuka contained males, females and juveniles for most of the year, yet during the summer months females were in small numbers or absent. Vuiva Island had few females for most of the year, but in November 1980 had 55 females and 10 males around the shoreline. Mabualau Island had 40 females and 34 males in December 1981. Juveniles frequented different areas to adults and were found most often on rocky outcrops exposed to the sea and had a relatively deep water approach. The actual sex ratio of the population was difficult to determine unless the entire population was sampled.

(ii) Population Size

Saint Girons (1964) placed estimates of the populations on Petit Taenia and Signal Islands as 405 (292 to 665) and 1700 (871 to 35416) respectively. In each estimate there was a large standard error which indicated further investigations were in order. Herre and Rabor (1949) commented that "many hundreds or even a thousand and more" L. colubrina may be seen on Tailon Island, Philippines. Preliminary investigations in the present study placed the size of the population of L. colubrina on Sausau Island, in the order of a thousand (Guinea 1981).

The estimates obtained in the present study raised some interesting features. In April, the population was 1075 and in July it was 1106. Both population sizes were obtained using the geometric estimate (i.e. unequal catchability). The estimate with the best goodness of fit in January was 1398 obtained with the Poisson distribution (i.e. equal catchability). Unequal catchability has been classified by Cormack (1966 in Caughley,1977) into three groups. The first cause is an inherent property of the individual expressed by its behaviour. Secondly, the animals learn to avoid being captured. Finally, the animal was not given the opportunity to be recaptured.

In view of these, it was endeavoured to reduce or keep consistent cause number three. The island was patrolled as often as possible; always on the the high tide with at least one patrol at each low tide. Problems of one researcher covering the entire island were possible although not obvious. Because snakes were caused a minimum of disturbance in marking, cause number two was reduced. Detailed scale counts, measurements, and body temperatures were confined to snakes caught during the last twenty-four hours of each visit. Cause number one, being inherent in the individual and therefore the most difficult to detect, was likely to be significant in producing unequal catchability. The procedures of marking and patrolling were similar for the three visits and I conclude that the cause of the population displaying unequal catchability during two capture periods was due to changes in the behaviour of the L. colubrina population.

However, the geometric estimate for January, of 2612, had an acceptable Chi Square value of 1.42 ($P < 0.75$). One conclusion that could be drawn from this was that in January the adults spent a longer period on land, thereby having increased opportunity of capture (equal catchability). Alternatively the population in January had increased to 2162, by immigration to Sausau Island and the population displayed unequal catchability which was more the rule. The population dynamics of L. colubrina clearly requires further, more detailed investigation.

9. DAILY ACTIVITY PATTERNS

A. INTRODUCTION

Heatwole, Minton, Taylor and Taylor (1978) suggested a diurnal activity pattern for sea snakes in general, but also reported that some species were active at night. Further indications of diurnal activity came from Heatwole and Seymour (1975) who reported a diel rhythm of metabolic activity for six species of sea snake. Herre (1942) reported that the activity of L. colubrina was greatest in the late afternoon, at night and on dull cloudy days. Saint Girons (1964) related activity in this species to temperature and sunlight-seeking behaviour. Direct observations and track counts were used by Saint Girons (1964) to estimate the proportion of the population that moved from land to the sea and vice versa, at each high tide. The present study indicated that on land, L. colubrina displayed activity patterns that were closely linked with environmental cues which included the tidal cycle, rainfall and sunset.

B. METHODS

Incidental observations regarding periods of activity of L. colubrina came from observations on the islands of S.E. Viti Levu. The number of active snakes was recorded for each visit to the islands in the study area. These visits which were during daylight, coincided with high tide. More detailed observations on activity were made on Sausau Island. The time of sighting and the activity were recorded for each individual snake. The numbers of males and females that were moving during hourly intervals were recorded and plotted for each day of each visit to Sausau Island. The times of sunrise, sunset, high water, and showers of rain were similarly plotted for each day of my visit (April and July 1981 and January 1982). The mark and recapture data were analysed to determine the percentage of previously unmarked snakes recorded during each twenty-four hour period of each visit to Sausau Island. These previously unmarked snakes represented those individuals that had arrived on the island within the last twenty-four hours.

C. OBSERVATIONS AND RESULTS

Observations on the concurrent movement of snakes came from Leleuvia Island where after a shower of rain at sunset, ten male _L. colubrina_ emerged from the forest onto the beach. This coincided with high water. Only ten snakes had been sighted on the island during the preceding afternoon. All had been resting and appeared reluctant to move.

The management of Toberua Island Resort reported that a large numbers of _L. colubrina_ emerged from the water after sunset on 22 September 1981. Their emergence coincided with high water. Within a few minutes 43 specimens had been collected by the staff from around a single guest house. This caused some alarm amongst the guests. These specimens were delivered to USP some days later. Many had died in transit and were in an advanced state of decay.

The number of male and female snakes active during each hour of each day of the investigations on Sausau Island are shown graphically in Figure 17. While ashore, _L. colubrina_ displayed periods of inactivity which were interrupted by some members of the population in response to sunset, high water and showers of rain. There was little response to sunrise. Snakes emerged from the water when the flooding tide reached the shore. This was usually two hours prior to the peak of the tide.

(i) Crepuscular Activity

A number of individuals became active at sunset. Males were usually the first to emerge from their resting places and remained active longer. During these periods of activity the snakes moved about in no definite pattern. A male under observation moved around for six hours after dark and did not leave area in which he was first observed.

(ii) Tidal Cycle of Activity

Individuals moved from the land to the sea and vice versa during high water. They appeared reluctant to cross the reef flat when it was exposed during the day. Snakes returning to land emerged in groups which suggested that they had congregated at sea to come ashore with the tide. The departure from land was less synchronized. Snakes moved from positions on the island from which the state of the tide could not be observed. Not all the snakes that were active at high water moved to the sea. Some which had been previously marked and recorded as active during high water, were subsequently recaptured on land after the tide had receded.

(iii) Response to Rain

Snakes became active during showers of rain. Some drank rainwater from hollows and depressions while others flicked their tongues at raindrops and wet vegetation. Showers of rain initiated wide spread activity amongst the population.

Those snakes not involved in activity remained asleep for up to four days. During this time there was no change in their position. Few individuals rested in the open for long. Even in the mangrove regions where a closed canopy provided shade throughout the day, individuals moved into crevices, hollow logs or climbed into the lower branches of the mangroves. Others coiled within clumps of vegetation. This thigmotropic behaviour indicated a preference for 'secretive' resting positions. In the majority of such positions, they were not completely concealed. Many snakes had a small amount of their body still visible to the researcher. In some cases this portion received either direct or diffuse sunlight during the day.

The method of counting tracks to estimate the number of snakes which moved daily to and from the sea proposed by Saint Girons (1964) was unsatisfactory for Sausau Island. The sand beach was only a small portion of the shoreline and most of the snakes were in adjacent mangrove areas. The percentage of previously unmarked snakes which were recorded for each capture day were fitted to the form of the equation presented by Limpus, Fleay and Baker (1984) for annual recruitment of the flatback turtle (Chelonia depressa) in Queensland. The percentages of each day's catch which were previously unmarked, were fitted to the form of the equation, $y = a + b \times c^x$ until the best goodness of fit (minimum Chi Square value) was achieved. The recruitment rate (in this study, percentage of unmarked individuals each day) is approximated by the asymptotic value ('a' $\pm$ the standard error of the estimate of 'a').

The graphs which were produced are shown with the data in Figure 18 (a,b,c). The equations produced are as follows:

April; $y = 80 + 50 \times 0.4^x$ (Chi Square = 0.02; dof = 2; $P < 0.99$)

July; $y = 91 + 50 \times 0.2^x$ (Chi Square = 0.03; dof = 3; $P < 0.995$)

January; $y = 72 + 100 \times 0.3^x$ (Chi Square = 4.71; dof = 7; $P < 0.75$).

The asymptotic values represented the percentage of the population which moved onto the island each day. Presumably, a similar percentage moved from the island during the same period. The percentage of the population which was involved in this daily movement was; April, 80 $\pm$ 1.7%; July, 91 $\pm$ 1.8%; and January; 72 $\pm$ 10.2%.

D. DISCUSSION

Three independent phenomena produced activity within the terrestrial L. colubrina populations on Sausau Island. A proportion of the population responded to the decrease in either temperature or light intensity at sunset. High tide brought about activity with individuals moving to or from the water. Other snakes moved for no apparent reason when the tide was full. Showers of rain initiated movement. This could have been because of the availability of freshwater. Drinking was commonly observed during and after rainfall.

Shine (1979) related daily movement in terrestrial elapids to foraging strategy. This would account for the movement associated with high tides. At sea, L. colubrina displayed searching or foraging behaviour as described by Shine (1979) for terrestrial elapids. A similar strategy could be involved in locating drinking water after a shower of rain.

Crepuscular activity enabled the individuals to find resting sites when the danger of exposure to lethal temperatures was at a minimum. At the same time lower body temperatures could have been elevated by conduction with warmed sand.

The estimate of between 72 and 90% of the population on the island changed its habitat each day, indicated that _L. colubrina_ moved more frequently from the land to the sea, and vice versa, than that of 7 snakes per tide for a population of 233, which was suggested by Saint Girons (1964). The smallest amount of movement from the island was in January i.e. 72 ± 10.2%. This supports the theory in Chapter 8; that the population spent longer on land in summer, thereby displaying equal catchability. The seasonal and daily activity patterns of _L. colubrina_ require further investigation.

10. PREDATION AND MORTALITY

A. INTRODUCTION

Common belief maintained that sea snakes had few predators because of their warning colouration (banded sea snakes and *Pelamis*), noxious taste (*Pelamis*) or because of their potent venom (Dunson 1975). As research continued into the ecology of sea snakes, more predators were identified. Heatwole (1975) gave a comprehensive list of sea snake predators including sharks, bony fish, birds of prey, crocodiles and invertebrates. Herre (1942) recorded moray eels as sea snake predators. Harding (1981) reported a live banded sea snake in the jaws of a carpet shark (*Orectolobus* sp.). Rancurel and Intes (1982) reported the presence of *Aipysurus* and *Laticauda* amongst the stomach contents of juvenile tiger sharks (*Galeocerdo cuvieri*) in New Caledonia. The following obvservations were made on populations of *L. colubrina* in the study areas in Fiji.

B. METHODS

For each specimen observed throughout the study, notes were kept as to the nature and the position of any scars or signs of predation. As the presence and the position of any scars formed part of the mark and recapture studies on Sausau Island a large number of observations came from that population. When dead or moribund individuals were encountered, close inspection and dissection were conducted in an endeavour to reveal the cause.

C. OBSERVATIONS AND RESULTS

(i) Predation

During the flooding tide of the afternoon of 8 July 1981, a juvenile *L. colubrina* (s-v length = 34.5 cm, weight =18 g) was observed struggling in a tidal pool on Mabualua Island. Closer examination revealed that the specimen was held by the tail by an immature female portunid crab (*Thalamita* (*crenata* ?)). The crab had secured the snake in its claws and had eaten the flesh thus exposing the backbone. As the snake was still alive and struggling violently, I freed it from the crab and set it on the side of the pool to photograph it. Again it was attacked by the crab which pulled it into deeper water. There, the crab continued to eat the flesh from the tail (Plate 14). The crab weighed 13 grams and was possibly two thirds adult size. This was an example of predation and not of scavenging dead sea snakes as reported by Heatwole (1975).

Another two specimens with similar mutilations were collected in 1981. Both were 37 cm in length and were carried ashore with the tide on Vuiva and Mabualau Islands.

(a) Scars

Heatwole (1975) suggested that the amount of damage incurred by an individual was an indication of the level of predation. Pernetta (1977) stated that the higher frequency of scars on L. colubrina from Mabualau Island was related to the large number of sea birds (Sula sula) nesting on the island. An examination of the regurgitated food items below the birds' nests on Mabualau Island revealed squid and small fish to be the major food items; there was no evidence of sea snakes being taken as food.

Statistical analysis of the frequency and position of scars on specimens from Sausau island during January 1982 revealed that of the 466 specimens for which records were kept, 93 (20%) had noticeable scars. There was no significant difference between the frequency and the position of scars on males and females (Chi square = 2.08, dof = 2, $P < 0.05$). Of those animals with scars, 9% of the scars were on the head, 32% on the body and 59% on the tail. The frequency of scars on adults and juveniles was not significantly different (Chi Square = 2.08, dof =1, $P < 0.05$). Four specimens had truncated tails, of which two were severed just posterior to the vent which produced the 'bob-tail' condition reported by Heatwole (1975).

The origin of the scars was unclear as most were healed; only one specimen had a fresh wound. The shape and size of the wound was consistent with having been slashed with a sharp blade; a boat's propeller or the lateral caudal keel of a mackerel or such fish. A diet of aggressive and formidable eels could cause damage to the snakes during feeding. Alternatively, the injuries of L. colubrina could be attributed to its terrestrial habit because Hydrophis melanocephalus, which occurred in the same waterways and shipping channels as L. colubrina, had very few scars (personal observations). Dangers associated with the terrestrial habitat could include any of the following. The weathered limestone topography of Mabualau Island was particularly sharp and capable of inflicting wounds. The intertidal region through which the snakes passed to and from the island had numerous crabs feeding during the incoming tide. An unexpected danger was encountered on Leleuvia Island where a male (s-v length = 70 cm) had crawled through the aperture of a shell (Turbo sp.) from which the whorl had been removed. The shell was lodged securely around the snake about one third along the body and had cut through the skin. This prevented the snake from swallowing and could have led to its death. The shell was broken with pliers and the specimen released.

A common scar of the snakes on Sausau Island was that of two parallel wounds that encircled the body about 2 cm apart (Plate 15). The circular nature of the scars suggested a crab predator. During high tide large crab claws often emerged through the extensive mats of floating Rhizophora seeds that collect in the mangroves. L. colubrina moved over and through these mats when passing to and from the shore.

(b) Ectoparasites and Commensals

The tick, Amblyomma nitidum Hirst and Hirst (Plate 1), was common in all populations of L. colubrina in the study areas. Infestations were as high as twenty per snake in some instances. The tick appeared to survive sea water submersion; snakes returning to land had live ticks attached. A single specimen from Sausau Island had small pin head sized mites attached between its scales on the tail. These have not been identified.

Specimens were generally free from fouling organisms. The barnacle, Platylepas ophiophilus Lanchester, was not found on L. colubrina although it was present amongst H. melanocephalus populations in Fiji. No specimen was fouled to an extent which would hinder either locomotion or feeding. Two Sausau specimens had small growths of green alga, Enteromorpha sp., attached to their scales. This alga was common in the mangrove environment in which these snakes were caught.

(ii) Mortality

From observations on the populations of the study areas there were three identifiable causes of mortality in _L. colubrina_.

(a) Fire

In July 1981 a grass fire on Sausau Island killed 35 specimens. Many of the 19 males and 12 females and 4 unidentified snakes which were killed, were coiled in resting positions (Plate 16). The fire which covered an estimated 500 square metres had apparently escaped from an open fire place used by local fishermen. The incident occurred some days before my arrival; the fire had burnt out and fresh grass shoots had emerged. The fire possibly moved so quickly as to catch the resting snakes unaware or _L. colubrina_ may have no innate fear of fire as was evident by several snakes investigating the open fire at my camp.

(b) Exposure

Several records were obtained of snakes leaving the water during overcast conditions and resting under light vegetation. A sudden clearing of the cloud cover left the resting snakes exposed to full sunlight. Snakes which had rested in open areas during such mornings were found to have died during the day. These snakes may have been sick and not able to reach proper shade, but this was not evident in subsequent dissections. Such cases of death by exposure came from Mabualau and Sausau Islands.

(c) Dehydration

Specimens kept in sea water in the laboratory became distressed and on their release drank freshwater. Gorman _et al._ (1981 p349) stated "it seems unlikely that rainfall would directly affect marine snakes". In the 80 days prior to my visit to Sausau in July 1981, a total of 45 mm of rain had been recorded at Vavalagi (6 km away on Vanua Levu). In the absence of rain and surface runoff from Vanua Levu, individuals were active in the early evening moving amongst the vegetation. Others removed droplets of water that accumulated by guttation on the leaves of plants (Plate 17). During the brief showers of rain that fell during my stay on the island, the snakes became active and drank rainwater that had accumulated in coconut leaves and shells. An individual was observed upside down in a one metre high shrub, licking, from its snout, the water that ran down its body.

It was obvious that the snakes were actively seeking water. The dead specimens that did not have burns from the fire (mentioned above) found on the island, could have died from dehydration. This aspect of their behaviour has not been reported previously and I conclude therefore that further research needs to be conducted into the freshwater requirements of sea snakes.

(d) Unknown causes

Moribund specimens were found in all populations throughout the year. The cause of their condition was not obvious. Externally, they had few ticks and had no visible sign of damage. They usually lacked condition and remained in the same position for days. Internally, there was no single identifiable cause. They had little if any body fat and the viscera was in a state of breakdown with the mesenteries broken in places. Bile which had escaped from the gall bladder and passed through the body wall, stained the ventral surface green. The average s-v length for a sample of moribund males taken to the laboratory for dissection was 70.6 cm (s.e. = 11.5, N = 3). Females had an average length of 111.6 cm (s.e. = 3.65, N = 10).

D. DISCUSSION

The colouration of L. colubrina was suggested to be aposematic and Heatwole (1975) predicted that they should have few predators. However 20% of the Sausau Island population had scars which could have been interpreted as attempted predation. Heatwole (1975) recorded that the frequency of scars within other sea snake populations was in the order of 10 - 25%. The major predators listed by Heatwole (1975), with the exception of birds, were marine and L. colubrina could escape predation by leaving the water. The populations in the present study were free from the introduced mongoose (Herpestes auropunctatus)

(Guinea, 1981), feral dogs and cats.

Juveniles were vulnerable to a number of predators not previously recorded. The portunid crab (Thalamita crenata) and possibly other crab species, was capable of capturing juvenile L. colubrina in shallow water. Although the entire snake is not devoured, the attack resulted in the death of the individual. This could explain the preference shown by juveniles for rocky areas with relatively deep (about 1 metre) water access.

The distribution of scars was consistent with the concept of attempted predation. Wounds to the head were more likely to result in death than those to any other part of the body. Juveniles had the same frequency of scars as the adults which indicated the period of maximum predation was in the first year of life. Infestations of the parasitic tick, Amblyomma nitidum, did not obviously decrease the health of the snake because obviously healthy specimens carried several ticks as did most of the L. colubrina population.

Apart from predation, mortality occurred from natural phenomena such as fire, exposure and dehydration. There was no evidence of direct human interference with the Fijian populations of L. colubrina as reported by Saint Girons (1964) for New Caledonia. The presence of moribund specimens of various sizes and presumably ages throughout the year, remained unexplained and would be worthy of further investigation.

11. TEMPERATURE RELATIONS

A. INTRODUCTION

Many reptiles have the ability to thermoregulate by a variety of behavioural and physiological mechanisms with the result that their body temperatures are often considerably different from those of the adjacent medium (Heatwole 1976). Considerable research into the body temperatures of the yellow bellied sea snake (*Pelamis platurus*) revealed it to have a body temperature within one degree of the surrounding water temperature (Dunson and Ehlert 1971, Graham 1974). The three species of sea snake, *Aipysurus laevis*, *A. duboisi* and *Emydocephalus annulatus*, studied by Heatwole (1981) had body temperatures the same as, or within 0.2°C of the temperature of the water where they were captured. Saint Girons (1964) indicated that the thermal optimum for *L. colubrina* in New Caledonia was 29 - 30°C. The minimum voluntarily accepted temperature was 12°C and the maximum was 33°C. Heatwole (1981) found that the mean upper temperature tolerance was 39.7° for *L. colubrina*.

B. METHODS

In the present study, all temperatures were taken with a slim bulb thermometer (Casella London BS2842/66 19397 10 - 65°) designed for a psychrometer. Snakes were captured by hand and had their temperatures taken immediately. The bulb of the thermometer was inserted into the intestinal tract via the cloaca. Body temperatures were taken from a sample of individuals engaged in a variety of activities e.g. swimming, resting and moving on land. The environmental temperature was recorded for each snake. For those captured in water, the water temperature was recorded in the immediate vicinity. The air temperature was recorded for resting and individuals moving on land. In addition, the ground temperature was recorded for resting individuals.

C. RESULTS AND OBSERVATIONS

A summary of the data is presented for L. colubrina in water, resting on land and moving on land in Table 18 and graphically in Figure 19 (a - d).

(i) In Water

The body temperature of snakes captured in water were in close agreement with the temperature of the water. As the majority of these measurements were taken when snakes were returning to land over the reef flat, the animals may have moved from cooler deep water to warmer shallow water. This factor could account for some slightly lower body temperatures.

(ii) On Land

The body temperatures of snakes on land showed greater divergence from the environmental (air and ground) temperatures. Explanations for these deviations came from observations on several groups of snakes having higher body temperatures than expected.

A cluster of snakes were found in the shade at the base of a tree on Mabualau Island on 23 August 1981 (time = 13:41hrs, air temp = 25°C). The group of 12 males and 3 females were entwined. All were adults. Average male s-v length was 82.3 cm (s.e. = 0.99, range = 77 - 89 cm) and average female s-v length was 133.7 cm (s.e. = 0.61, range = 133 - 134.5 cm). The temperature within the cluster was 28.5°C. The average body temperature was 29.1°C (s.e. = 0.47, range = 27 - 34.5°C). The cluster was in a position where it would not have been in the sun at any time during the day. The increased body temperatures could have been brought about by warmer individuals moving into the group or alternatively by a combination of metabolic and muscular activity.

A second observation was made on Mabualau Island on 18 October 1981. An adult male (s-v length = 97 cm) was observed beneath a rock. A length of his body equivalent to two black bands was in direct sunlight. During the following 20 minutes of observations, the snake moved several times. Each shift forward brought different bands into the direct sunlight. When the animal was collected, it was noticeably warm in the region of the heart (near the tenth band), being the position exposed to direct sunlight. The body temperature was 31°C; that of the sand beneath the rock was 27°C. The air temperature in the shade was 26°C and the surface temperature of the rock in direct sunlight was 50°C. By having a small portion of its body in direct sunlight and the remainder in contact with cool sand the snake appeared to regulate its body temperature to the optimum suggested by Saint Girons (1964).

D. DISCUSSION

Heatwole (1981) reported that either on land or in the sea, the body temperature of _L. colubrina_ closely approximated that of the environment. The present study revealed that in water, the body temperature of this species ranged from 1°C to 1.5°C below the water temperature. Any heat generated or gained by the snake would have been quickly dissipated to the water because of its higher thermal conductivity than air. The movement of snakes from warmer or cooler bodies of water could account for the recorded temperature differences.

On land _L. colubrina_ was capable of attaining body temperatures higher than those of the air and the substrate. Heatwole (1981) recorded a maximum difference between body and environmental temperatures of 0.8°C for _L. colubrina_ resting on land. The maximum difference recorded in the present study was 7°C. _L. colubrina_ was capable of regulating its body temperature closer to the optimum than was previously recorded by Heatwole (1981).

Lillywhite (1980) described behavioural thermoregulation in seven species of Australian elapid snakes. Thermal regulation was achieved by the snakes shuttling to and from the heat source or by adjusting the snake's position or orientation while basking. Lillywhite did not observe flattening or tilting of the body during basking as was reported by Heatwole and Johnson (1979) for _Pseudechis porphyriacus_. Neither flattening nor tilting of the body was observed in the present study, as part of the normal thermoregulatory behaviour of _L. colubrina_. However, temperatures as low as those recorded by Heatwole and Johnson (1979) are not normally found at sea level in Fiji.

Shuttling, as such, was not observed in _L. colubrina_ populations in the present study, although it may have occurred incidentally by snakes moving through areas of full sunlight and shade.

Coil adjustments while resting in semi-shaded positions were observed as described above. It is possible that the banded colouration of _L. colubrina_ may have some effect on the amount of heat energy gained by basking. This aspect of the thermoregulatory behaviour of _L. colubrina_ requires further, more detailed investigation.

Thermoregulation was socially enhanced by aggregations where the average body temperature of the individuals (29.1°C) was four degrees higher than that of the environment. The thermal preference for this species appeared to be around 30°C as suggested by Saint Girons (1964). Individuals with body temperatures between 21 and 34.5°C were active. Body temperatures below 21°C were not recorded. The environmental temperatures recorded during the study indicated that _L. colubrina_ were not exposed to dangerously low temperatures in Fiji.

12. VENOM APPARATUS

A. INTRODUCTION

Voris (1972) related the morphology of the skull of sea snakes to specialisation in feeding. Laticauda, according to Voris (1972), was a relatively short thick sea snake which had a cobra-like skull with relatively long fangs (mean length = 2.5 mm). Descriptions of the venom glands and fangs of sea snakes have been recorded by Limpus (1978a) and Halstead (1978). Neither author dealt with Laticauda colubrina. A study of the gross morphology of the venom gland, fangs and teeth of L. colubrina, was conducted on several adult female specimens that were chosen indiscriminately from the laboratory specimens. Females were used because of their larger skulls.

B. METHODS

(i) Venom Gland

The heads were severed from six, adult, female L. colubrina that had been frozen. After thawing to room temperature, the skin was cut posterior to the venom gland on each side of the head and elevated to expose the venom gland. Indian ink was injected into the lumen of the venom gland and gentle pressure applied until the ink was visible on the tip of the fangs (Limpus 1978a). The venom duct was at that stage filled with ink and quite distinct from the surrounding tissue. The skin covering the supralabial scales and the rest of the head was carefully removed. The skulls were cleared in 1% potassium hydroxide solution and stained with 0.01% Alizarin Red S solution as described in Dawson's Method of staining bones in small vertebrates in Gurr and Florey (1962 p 125). The preparations were then cleared in potassium hydroxide (1%), glycerin (20%) solution and stored in pure glycerin.

(ii) Fangs and Teeth

Alcohol-preserved heads were skinned and soaked in freshwater for three days before being placed in freshly prepared 6% sodium perborate solution for a further 24 hours (Limpus 1978a). This method gave clean preparations but the original articulation of the bones was lost and any fangs and teeth that were not cemented (ankylosed) were dislodged.

C. RESULTS

(i) Venom Gland

The venom gland was positioned posterior to the eye and above the pterygoid bone. The adductor externus superficialus was dorsal to the venom gland and contiguous throughout its length. The posterior portion of the adductor externus superficialus was attached to the quadrate bone. The venom duct which exited the anterior portion of the venom gland, moved forward beneath the eye in the supralabial position and terminated at the base of the fang. Plate 1B shows the relative positions of the venom gland, the path of the venom duct, the position of the functional fang and the venom canal within the fang.

(ii) Fang

A single fang was cemented to the maxillary bone. Beside it lay a crater-like depression which in one preparation contained a poorly cemented replacement fang. The functional fang was cemented in either the inner or outer of the two positions. Therefore, space was available for two fangs at the anterior of the maxillary bone, but it was normal for only one fang to be cemented into position. Posterior to a well defined diastema, a single, solid, grooved tooth was cemented to the outer edge of the maxillary bone. There was only one position for this solid tooth on the maxillary bone.

Several reserve fangs were within the mucous membrane immediately posterior to the fang. These reserve fangs numbered up to six and appeared in order from a fully developed but uncemented fang, closest to the functional fang, to immature fangs of less then a millimetre in length with only the tip and the discharge orifice developed. The functional fang was smoothly curved with the entrance lumen to the fang and the discharge orifice on the anterior surface. Joining these two openings in the fang was a noticeable groove on the anterior surface. The groove resulted from the the complete sealing of the lateral folds of the fang to form a closed tube (venom canal). A single fang, out of the twelve examined, had this canal incompletely covered. This produced a grooved fang.

Several fangs had chipped tips. One skull possessed a fang that was in the process of replacement. The functional fang was in position; a poorly cemented secondary fang occupied the depression beside it.

The length of each fang was measured in a straight line from the base of the fang (proximal edge of the entrance lumen; Limpus, 1978a) to the tip using a vernier caliper. The mean fang length was 2.7 mm (s.e. = 0.06, n = 12, range = 2.6 - 3.6 mm).

(iii) Teeth

Small solid teeth were positioned on the palatine, pterygoid and dentary bones. Crater-like depressions were obvious where teeth were missing. The palatine bone had positions for five teeth. The number of teeth in position ranged from two to five with the mean being 3.4 (s.e. = 0.45, n = 12). The pterygoid bone had between fifteen and eighteen positions (mean = 16.4, s.e. = 0.25, n = 12) of which between eight and fourteen teeth were present (mean = 9.9, s.e. = 0.67, n = 12). The dentary bone had positions for twelve to fifteen teeth (mean = 13, s.e. = 0.2, n = 12) of which between six and ten were present (mean = 7.7, s.e. = 0.36, n = 12).

D. DISCUSSION

Descriptions of the skull of L. colubrina were given by Smith (1926), Voris (1972) and Mao and Chen (1980). The position size and shape of the venom gland from the present study are in agreement with those given for L. colubrina by Mao and Chen (1980). As no histological investigation was conducted, few comparisons could be made with those presented by Limpus (1978a), although the position and external morphology were in agreement.

Limpus (1978a) was critical of the interpretation and description of the venom duct by Halstead (1978 pp 930 Figure 3) where the venom duct was illustrated as dividing posterior to the functional fang and a branch of the duct entered the reserve fang. Plate 18 shows that in L. colubrina the venom duct was single and and did not divide to supply the reserve fang, but curved around the front of the maxillary bone before terminating at the base of the functional fang. There was no evidence of the venom reservoir and ductule as depicted by Halstead (1978 pp 933, Figure 5a). Instead the venom duct emptied into the gingival sulcus formed by the surrounding mucous membrane which in the preparation formed a seal around the shaft of the fang and directed the ink (presumabely venom) into the entrance lumen and to the venom canal.

This study supported many of the observations of Limpus (1978a) who examined the fangs and venom glands of eight species of Australian sea snake. Laticauda colubrina shared many of the features attributed to sea snakes, and demonstrated by Aipysurus laevis, Astrotia stokesii and Disteira major (Limpus 1978a). These features included; two positions were available at the anterior of each maxillary bone for fang placement. The functional fang was ankylosed in either position. The fang was curved with the entrance lumen at the anterior base and the discharge orifice at the anterior tip. These openings were connected by a venom canal formed from the lateral folds of the fang which produced a groove on the surface. Posterior to the functional fang and surrounded by mucous membranes were the replacement fangs which ranged in size from mature and ready to be cemented, to immature fangs showing just the tip and the discharge orifice.

Unlike the hydrophiids described by Limpus (1978a), L. colubrina had only one solid tooth per maxillary bone. Smith (1926) described Laticauda as having one or two teeth following the fang. Smith's (1926 p x) drawing (after Boulenger) illustrated two solid teeth on the maxillary bone, as did that of Mao and Chen (1980 p 28). The palatine, pterygoid bones of the upper jaw and the dentary bone of the lower jaw each carried posteriorly curved teeth. Not all of these teeth were ankylosed into position; some were dislodged during preparation. Numerous small replacement teeth were in the mucous membranes adjacent to each of the bones. Fang replacement appeared as continuous waves along each row of teeth (Limpus 1978a) because alternate teeth were missing in most preparations. With the exception of the maxillary teeth, the number of teeth positions on each bone were in agreement with those reported by Mao and Chen (1980) for Taiwanese specimens of L. colubrina (palatine, 5 - 6; pterygoid, 14 - 17 ;dentary, 11 - 12). Several teeth and fangs, in the present study, had chipped tips similar to that reported by Limpus (1978a).

The length of the functional fangs (2.6 - 3.6 mm) and their fully enclosed venom canal plus the toxic venom (Chapter 13) made L. colubrina a well equipped predator of eels and a potential danger to man. Further investigations into the method of fang and tooth replacement by L. colubrina could prove fruitful. Regardless of its potential danger to man, L. colubrina had a docile nature and appeared reluctant to bite when handled.

13. TOXICOLOGY

A. INTRODUCTION

The following chapter has been published (see Singh and Guinea, 1984). Study of the toxicity of the venom formed part of the present study and was reprinted below for the completeness of this thesis.

Although envenomation from sea snakes (Hydrophiidae and Laticaudidae) has been a potential hazard to humans throughout the Indo-Pacific region, the incidence of sea snake bite has been difficult to assess. This was due to victims being either fishermen or villagers who did not seek medical assistance or who failed to report the incident. In many Pacific island countries complete records of sea snake bites have not been kept even when reports have been made.

One of the few cases of envenomation by this species was that of a 14 year old boy who was bitten on the hand by a five foot specimen on Nukulau Island near Suva (Fiji Times, 1978). Within an hour his tongue swelled, followed by general paralysis of the body and convulsions. Three days later, recovery was complete except for a slightly swollen hand.

The low incidence of reported envenomation from this species has been attributed to two beliefs: the docile nature of the animals and the presumed low toxicity of the venom. Although the former has been documented (Smith, 1926; Saint Girons, 1964; Pernetta, 1977), the latter has not been investigated extensively. Bail and Rageau (1958) recorded their observations on the experimental envenomation of two rats by L. colubrina. As the rats showed no signs of illness the toxin of this species was thought to be harmless. Halstead (1978) reported on the work of Smith and Hindle (1931) and Tu et al. (1962). Both authors were involved with studies on the toxicity of L. colubrina venom. Wright (1969) described the effect of crude L. colubrina venom on domestic fowl. Levey (1969) found the venom of specimens collected in Malaysia had a toxicity and yield similar to that of specimens from Singapore reported by Smith and Hindle (1931).

The present study was undertaken to obtain comparative data for L. colubrina found in Fiji, to ascertain the effect, if any, of fresh water deprivation on venom yields, and to characterise the mode of action of the venom on skeletal muscle of chicks.

B. METHODS

(i) Venom Collection and Storage.

The snakes used in this study were captured on Toberua Island and transported to the laboratory in Suva the next day. The snakes were maintained in cages without food. The ambient room temperature for the period of study ranged between 20 and 28°C which was within the range of environmental temperatures for this species at that time of the year.

A review of the literature indicated that of the factors which affected venom yield, no data were available on the effects of fresh water deprivation. As these snakes have been observed to drink fresh water in the wild, it was decided to incorporate this parameter in the present study. Venom extraction began on 32 specimens which were all collected on the same day (August 24,1981). During the period of the study some specimens were excluded because of either a loss of condition or, if during manipulation, venom could not be extracted or was lost. Eventually, two groups were identified: Group I of nine animals (2 males and 7 females) which were maintained without food but allowed tap water _ad libitum_ from their time of capture; Group II of eight animals (1 male and 7 females) which were maintained without food or water. Both groups of snakes were kept in the laboratory for eight days before their first venom extraction on September 1,1981. Subsequently, venom extraction was performed on three more occasions at weekly intervals (September 8, 15 and 22).

As the amount of venom elaborated by this species was small by comparison with many of the terrestrial _Elapidae_, care was taken not to touch the fangs and adjacent membranes for fear of premature venom release. Apart from the method of holding the mouth open, the procedures for venom extraction were similar to those used by Limpus (1978a). The mouth of the snake was forced open and the jaws dislocated to expose the fang on either side. A length of clean plastic tubing (internal diameter = 0.58 mm) was carefully placed over each fang in turn (Plate 19). As the tubing slid over the fang, it pushed the mucous membranes proximally. In a few cases venom release occurred immediately the membranes were touched. Venom release was only from the side being treated. In other cases, and to increase the yield, finger pressure massage was applied to the skin overlying the appropriate venom gland. The fang and gland on the other side were similarly manipulated. Usually the amount of venom collected from both fangs was more than could be accommodated in the length of plastic tubing and the excess was drained into a small glass vial. With appropriate weighings of the plastic tubing, and the vial before and after collection of the venom, the wet weight yield was determined.

The vial with the plastic tube inside it was frozen and then lyophilised using a Chem Lab Instruments freeze dryer (model SB 6) until constant weight of venom was obtained. This usually required 5-6 hours. The sealed vials of lyophilised venom were weighed to determine the dry weight yields and then stored at -10°C in the dark until required. The volume of the venom was determined by subtraction of the dry weight yield from the wet weight yield. This provided the weight and volume of the liquid fraction of the venom.

(ii) Nerve-Muscle Preparations.

Biventer cervicis nerve-muscle preparations were isolated from chicks 4-10 days old (Ginsborg and Warriner, 1960) and mounted in 50 ml organ baths with a resting tension of approximately 0.5 g in Krebs-Henseleit solution (NaCl, 6.92; $CaCl_2$, 0.28; KH_2PO_4, 0.16; $NaHCO_3$, 2.1; dextrose, 2.0 g/l). The solution was maintained at 38°C and gassed with oxygen containing 5% CO_2. For indirect stimulation, contractions were elicited by stimulating the motor nerve in the tendon at a frequency of 0.1 Hz by square wave pulses of 0.2 msec duration and strength greater than that required for maximal contractions. Responses similar in size to the twitches were obtained for submaximal contractions of acetylcholine ($1\text{-}8 \times 10^{-4}$ M), carbachol ($1\text{-}5 \times 10^{-5}$ M) and KCl ($2\text{-}5 \times 10^{-2}$ M) in the absence of nerve stimulation. Acetylcholine and KCl were allowed to remain in contact with the tissue for 30 seconds and carbachol for 60 seconds. Some preparations were stimulated directly by placing the electrode in contact with the belly of the muscle and using 1 msec supramaximal pulses. In these preparations neural transmission had been abolished by prior exposure to 3 µM tubocurarine. Contractions and contractures were recorded isometrically on a Grass 79 polygraph using Grass FT03 force-displacement transducers.

(iii) Toxicity Studies in Mice.

Solutions of crude lyophilised venom for injection were prepared in 0.9% saline with the concentration adjusted such that an injection volume of 0.10-0.15 ml could be used throughout the experiment. Male albino mice (CFI, 28-35 g) were injected intra-peritoneally (i.p.) with doses of the venom ranging from 0.1 to 3.0 mg/kg (8 mice per dose). Controls were injected with 0.1 ml of 0.9% saline. In no instance did control mice display any toxic symptoms after injection. The venom-injected mice were observed continuously for a four hour period following injection, then at hourly intervals for a total of eight hours, then at six hourly intervals for a total of two days. The LD_{50} for the venom was determined by interpolation from a semi-logarithmic plot of mortality vs. venom dose.

C. RESULTS

(i) Venom Collection

a. Appearance of the Venom.

In all cases the whole venom was a clear, viscous liquid which on freeze-drying formed a white solid. On some occasions there was some cloudiness in the last portion of the venom extracted from each fang.

b. Venom Yields.

The sex, snout-vent length (svl) and weight of each specimen and the wet venom weight, calculated volume, dry venom weight and percentage solid in the whole venom for the initial extractions from Group I and Group II are shown in Tables 19 and 20 respectively. The initial venom yields of the Group I and II individuals were compared with the sex of the specimens using a Two Way Analysis of Variance. There was no significant difference between wet weight venom yields and sex ($F = 1.23$; 1,13 df; $P < 0.25$). There was no significant difference between the wet weight yields of those with water available and those without ($F = 0.566$; 1,13 df; $P < 0.25$). Similarly there was no interaction between sex and treatments ($F = 0.027$; 1,13 df; $P < 0.25$).

The dry weight yields were also tested by the same procedures and indicated that no significant difference existed between sex ($F = 1.323$; 1,13 df; $P < 0.25$). There was no significant difference between treatments ($F = 0.409$; 1,13 df; $P < 0.25$). Again there was no significant interaction between sex and treatment ($F = 0.019$; 1,13 df; $P < 0.25$). There was a positive relationship between the snake weight and the wet yield for Group I and II animals combined. The regression equation of

$$Y = 2.11 + 0.06X$$

was obtained using the least-squares method: where Y was the wet venom yield (mg); X was the snake weight (g) and the regression coefficient (r) was 0.56.

Figures 20 and 21 show the values of the mean and standard error of the mean (s.e.) for the dry venom yields and percentage solid in the whole venom for the weekly extractions.

(ii) Chick Biventer Cervicis Nerve-Muscle Preparation.

The dried venom inhibited responses of the muscle to indirect stimulation (Figure 22). At low concentrations there was a delay of several minutes before any diminution of twitch height was observed and the blockade of twitches developed slowly. At higher concentrations the lag period was much shorter and the development of blockade faster. To obtain a quantitative assessment of the toxicity of the venom, the time taken for different concentrations to decrease twitch height to 50% of its control value was selected as a suitable parameter (Figure 23). The concentration-time curve was very steep. A 50% reduction in twitches was produced by 1 µg/ml in about 20 minutes whereas 0.1 µg/ml produced 50% reduction in about 140 minutes.

After complete blockade of twitches the preparations responded to direct muscle stimulation (Figure 22) and responses to raised concentrations of KCl were unaltered. This indicated that there had been no appreciable effect on the muscles themselves. However responses to acetylcholine and carbachol were completely abolished by the venom. The effects of 1.9 µg of venom per ml on responses to indirect stimulation, acetylcholine, carbachol and KCl are shown in Figure 24.

The effects of the venom were irreversible. Prolonged washing for up to five hours produced no recovery of responses to either nerve stimulation, acetylcholine or carbachol in preparations treated with venom.

(iii) Toxicity Studies on Mice.

After injection of the venom each mouse behaved normally for a time after release. In a mouse receiving a lethal dose, the eyes bulged a little, activity decreased, followed by a lowering of the head and thorax. At this stage the animal was unable to raise its body and could only push itself forward by frantic movements of the limbs. Breathing rate was much reduced; breathing was laboured. The breathing rate soon decreased to zero and death occurred with the animal showing flaccid paralysis.

The quantitative data for the mouse acute studies are shown in Figure 25. At all doses of the venom below 0.10 mg/kg i.p. no death occurred. Higher doses led to an increase in mortality and the lowest dose to give 100% mortality was 1 mg/kg. The LD_{50} determined by interpolation from the graph was 0.35 mg/kg and time to death at this dose was about 6 hours.

D. DISCUSSION

Various methods of venom extraction have been previously employed in yield studies in snakes. Among these are: injection of venom through a rubber diaphragm stretched over a collecting flask (Reid, 1956; Levey, 1969; Branch, 1981); exposing natural prey, e.g. a mouse, to a snake and estimating the amount of venom injected by weighing the mouse before and after the strike (Kochva, 1960); electrical stimulation (Johnson, 1938; Glenn, 1972) and gel diffusion-precipitation followed by an <u>in vivo</u> assay of the venom-containing tissue (Minton, 1969; Kondo <u>et al.</u>, 1972). None of these methods approximates the natural biting situation and such studies only give a relative assessment of the quantity of venom available from each animal. Morrison <u>et al.</u> (1982) elaborated further on this point. The present investigation was undertaken with due recognition of these constraints. Of the available methods of venom extraction, the one used in this investigation was selected as it gave better results for species with small fangs and low yields (Limpus, 1978a).

The absence of colour in the fresh venom of Fijian L. colubrina, and the white powder which arose from it when dry, agreed with the findings of Limpus (1978b) who sampled 48 specimens from eight species of sea snake from South Queensland waters, and of those of Reid (1956) who worked extensively on sea snakes of Malaysia. However, these findings contrasted markedly with the light yellow (dry) venom of L. colubrina from Singapore as reported by Smith and Hindle (1931). Barme (1968) reported the same colour for dry venoms of other sea snakes. Devi (1968) recorded the venom colour as orange when dried. The reason for this colour difference is not known but presumed by Limpus (1978a) to be related to geographic factors.

The sex and size of the snake have been mentioned as factors which affect venom yields (Reid, 1956; Limpus, 1978a). As adult male L. colubrina specimens are smaller in weight and snout-vent-length (SVL) than their female counterparts (Guinea 1981), they would be expected to give lower yields. Their yields were not significantly different from those of females, but were at the lower end of the regression for weight and yield. The small sample size of males and the variable yields from the females may not have given a true indication of the weight-yield relationship for this species.

Fang loss during extraction may have given lower yields for some specimens . During the initial venom collection (September 1, 1981) four specimens lost a fang. Only one had a substantial loss of venom in conjunction with the loss of the fang (Table 19). All four specimens had both functional fangs in place one week later (September 8, 1981) when the second extraction took place. One on this occasion lost the other fang and two other snakes lost fangs with one losing both. At the time of the third extraction all the snakes had both fangs present and lost none during the venom collecting process. By the time of the fourth extraction (September 22, 1981) one of the specimens that had lost the left fang on September 1, 1981 then replaced it, had lost the right fang. Two specimens that previously had no fang loss had a small fang in position. The loss of fangs was shared evenly between Group I and II specimens and presumed not to be affected by the treatment of the groups.

The wet weight yields and volumes were within the range reported for L. colubrina by Levey (1969) and for other sea snakes by

Reid (1956) and Limpus (1978a). The percentage solid values were also similar to that obtained by Levey (1969).

The mean dry yield for successive extractions from the two groups (Figure 19) differed to previous studies (Reid, 1956; Levey, 1969; Hokama, 1978; Limpus, 1978a) in which a gradual or sometimes a rapid fall in dry weight yields occurred with time. The dry weight yields of both groups in the present investigation increased over the period of the study. In the water supplied group (Group I) there was a marked increase in the second extraction and thereafter a smaller but not significant increase. The water deprived group (Group II) had a sharp increase in dry weight yield and this trend continued to the final extraction for which the dry weight of the venom yield was almost 250% of that for their first collection. This increase in yields was not shown in the corresponding percentage solid values for Group I individuals. The importance of freshwater intake by sea snakes has not been explored. Dunson and Taub (1967) described the function of the salt regulating gland of <u>L. semifasciata</u> but the dependence of <u>L. colubrina</u> on freshwater has not been resolved. Fresh water deprivation did bring about an increase in both volume and dry weight. This aspect of <u>Laticauda</u> physiology requires further investigation.

An unexpected low yield for the second extraction was given for both groups. Apart from a gradual decrease in the mean ambient temperature in the period between the first and second extraction (Figure 21B), there was no change in treatment which could account for this low value. Support for the decrease in percentage solid being temperature related came from observations made on a group of four snakes which were not part of the main experiment. These animals which were collected on September 2 and kept under the same conditions as Group II (water deprived) snakes, were processed on September 8, 15 and 22, dates which coincide with the second, third and fourth venom extractions in the main investigation. The mean percentage solid with standard errors for the three extractions were 26.5 $\pm$ 0.9%, 32.5 $\pm$ 0.8% and 32.6 $\pm$ 1.7%, respectively. The lowest mean percentage solid was obtained on the same date (September 8) as that for Group I and II snakes.

In the chick biventer cervicis preparation the dry venom reduced contractions elicited by the stimulation of the motor nerve and nicotinic agents, acetylcholine and carbachol. Muscle preparations continued to respond to elevated concentrations of KCl and to direct stimulation even after responses to indirect stimulation by acetylcholine and carbachol were completely abolished by the venom. These findings suggested that the venom acted at the level of the acetylcholine receptor to block neuromuscular transmission and had no direct action on muscle contractility. This concept that the venom molecules were bound irreversibly to the postjunctional acetylcholine receptor was supported when five hours of washing the preparation failed to restore muscle responses to direct stimulation. A fraction isolated from the venom of Laticauda semifasciata from the North West Pacific has been shown to act in a similar fashion by irreversibly blocking neuromuscular transmission in skeletal muscle preparations (Tamiya and Arai, 1966).

The action of the venom on laboratory mice was similar to that described for many other sea snake venoms (Barme, 1968). However, it did not cause convulsions or the formation of sticky secretions from the mouth and nose as recorded for L. semifasciata in mice, guinea pigs and rabbits (Tu, 1959) and for L. colubrina in mice (Levey, 1969).

The toxicity of a venom depends on the route of injection and the species of animal used. For instance, the LD_{50} values for i.v. injection of L. semifasciata venom are 0.21 mg/kg in mice, 0.063 in guinea pigs and 0.049 in rabbits (Tu, 1959). For s.c. injection with the same venom the values are 0.34 mg/kg in mice, 0.089 in guinea pigs and 0.21 in rabbits. In the present study L. colubrina venom gave an LD_{50} of 0.35 mg/kg when injected i.p. in mice. This compared favourably with previously reported values for the same venom in mice, i.e., 0.25 mg/kg s.c. (Smith and Hindle, 1931), 0.42 mg/kg s.c. (Tu et al.,1963), 0.45 mg/kg s.c. (Levey, 1969) and 0.40 mg/kg i.v. (Sato et al., 1969).

Smith and Hindle (1931) concluded that the small amount of dried venom produced by L. colubrina, 5.1 mg in their study, reduced the chance of human fatality by envenomation. Individual yields in the present study ranged from 2.8 mg to 35.7 mg, with the water deprived specimens producing 2.5 times that amount at the end of the study. The above data demonstrate that L. colubrina, in particular, and sea snakes in general yield venoms of very high toxicity. The low incidence of deaths from this species must be attributed to its docile nature and indifference to being handled rather than to its venom toxicity and venom yield.

14. CONCLUSION

Presented in this thesis are the findings of almost 20 months part-time research into the biology of Laticauda colubrina. Morphometric and reproductive data were collected from the populations which inhabited several islands in the vicinity of Suva, Viti Levu. Population studies were conducted on the more remote and uninhabited island of Sausau, Vanua Levu. It was not feasible to survey the entire Fiji Group, however stastically viable samples were presented for each aspect of the investigations.

Smith (1926) presented details of the morphology of L. colubrina, and concluded that geographic variation within the species could not be detected. With more research having been conducted in recent years i.e. Mao and Chen (1980) and the present study, comparisons can now be made using squamation and colouration e.g. ventral scale count and banding pattern, for populations in the North Pacific and those of the South Pacific. Pernetta (1977) stated that all of the differences, which he observed, between males and females were significant. The degree of significance was not given for any character. The present study demonstrated that there was no significant difference between some characters e.g. the position of the umbilicus, number of scale rows at neck, and the number of infralabial scales. The number of subcaudal scales were significantly different between males and females; this character was used for sexing immature specimens. The data from this study has been presented in a form which would enable further comparisons to be made when research has been conducted in other localities.

The reproductive biology of L. colubrina has been reviewed by several researchers. The mode of reproduction (Smith, 1930; Smedley, 1931 a and b), seasonality (Gorman et al., 1981), the number of clutches per season (Pernetta, 1977), the clutch size (Saint Girons, 1964), and the size at, and the age of sexual maturity (Saint Girons, 1964), have been questioned and discussed. In Fiji, L. colubrina was demonstrated to be oviparous with a well defined period of reproduction in the summer months. An average of six eggs were laid per clutch. There was nothing to indicate that more than one clutch was laid per season. Sexual maturity in females was reached at 98 cm (s-v l) at a proposed age of 26 months. Males were smaller (s-v l ≈ 70 cm) and younger (15 months) at maturity.

The diet consisted exclusively of two families of eels, Muraenesocidae and Muraenidae. Voris (1972) restricted the prey species to bottom dwelling eels and fish, and other forms associated with rock and coral outcrops. The size of the eels taken by some females were up to two-thirds of the weight of the snake. Similar observations have been made by Saint Girons (1964).

Members of the population became active in response to the daily cycles of high tide and sunset. Further activity was initiated by showers of rain. Between periods of activity, most of the population rested. Body temperatures below 21°C were not recorded. The thermal optimum, in this study, of about 30°C is in agreement with that proposed by Saint Girons (1964) and Heatwole (1981). Body temperatures above the environmental temperature were recorded for many snakes. These higher body temperatures were attained by basking and the formation of clusters of entwined individuals in cooler weather.

The feeding biology and seasonal rates of digestion, and their influence on the population dynamics of L. colubrina, require further investigation. Saint Girons (1964) proposed that this species spent possibly two weeks ashore digesting their prey in summer, and possibly more than a month in winter. The present study indicated that, in summer, approximately 72% of the terrestrial population moved to the sea in a twenty-four hour period. In winter, this figure increased to about 90%. Mark and recapture studies indicated that the population displayed equal catchability in summer and unequal catchability in winter. Three methods of estimating the size of the population were employed. The 'Petersen estimate' and that given by Schumacher's method were questioned because they required equal catchability. They did estimate that the largest population was present in January. The third method, 'frequency of capture models', accommodated unequal catchability, and estimates of the population on Sausau Island were; April, 1075; July, 1106; January, 1398.

Studies on the morphology of the fangs and the toxicity and mode of operation of the venom, indicated that L. colubrina had the potential to cause serious injury to, and possibly death of, a human victim of envenomation.

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TABLES

Authors	Taxon
Stejneger (1907)(Japan only) and Underwood (1967)	Elapidae Hydrinae (Hydrophiinae) - Laticauda, Emydocephalus, Disteira (Hydrophi and other genera.
Smith (1926)	Hydrophiidae Laticaudinae - Laticauda, Aipysurus, and Emydocephalus. Hydrophiinae - Hydrophis, and other genera.
Maki(1931) (Japan only)	Hydrophiidae Laticauda, Emydocephalus, Disteira (Hydrophis), and other genera.
Dowling(1967)	Elapidae Laticaudinae (Recent sea snakes). Hydrophiinae (Advanced sea snakes).
McDowell (1972)	Elapidae Hydrophiinae - Hydrelaps, Aipysurus, and Hydrophis groups (true sea snakes). Elapinae - Laticauda (false sea snakes), and terrestrial elapid genera
Burger and Natsuno (1974)	Elapoidea Laticaudidae (sea kraits - Laticauda. Hydrophiidae (sea snakes). Ephalophiinae (thick sea snakes) - Hydrelaps, Ephalophis, Parahydro Aipysurus, and Emydocephalus. Hydrophiinae (flat sea snakes) - Hydrophis, and other genera
Smith, Smith & Sawin (1977)	Elapidae Elapinae Laticaudini Laticauda (Sea Kraits) Hydrophiidae Hydrophiinae Ephalophini Ephalophis (Ephalophine Sea Snakes) Hydrelapini Hydrelaps (Hydrelapine Sea Snakes) Aipysurini Aipysurus (Aipysurine Sea Snakes) Hydrophiini Hydrophis (Hydrophid Sea Snakes)
Cogger, Cameron & Cogger (1983)	as per Burger and Natsuno (1974)

Table 1. The classifications of sea snakes (after Mao and Chen 1980)

I. Scales in 19 rows; no azygous praefrontal
shield; upper lip dark brown................ 1. *laticaudata*

II. Scales in 21 to 25 rows; normally an
azygous praefrontal shield.

A. Rostral not divided; upper lip yellow.... 2. *colubrina*

B. Rostral divided horizontally; upper lip
brown.

Ventrals 195 to 205; 30 to 42 bands on the
body .... 3. *semifasciata*

Ventrals 187 to 195; 18 to 31 bands on the
body .... 4.. *schistorhynchus*

Table 2. Key to the species of *Laticauda* (from Smith 1926 p3)

Fiji Museum Number	RA224	RA189
Sex	Female	Male
S-V Length (cm)	124	89.5
Tail Length (cm)	14	13
Black Bands	29	31
Mid-body Scale Rows	25	23
Subcaudal Scales	33 pairs	41 pairs
Weight (g)	995	393
Head Length	4 (1)	2.5 (1)
Heart	41 - 44 (10 -11)	32 - 35 (12.8 - 14)
Liver	44 - 74 (11 - 18.5)	35 - 57 (14 - 22.8)
Gall Bladder	79 - 82 (19.5 - 20.5)	61 - 62 (24.4 - 24.8)
Gonad (right)	82 - 91 (20.5 - 22.7)	70 - 72.5 (28 - 29)
(left)	93 - 100 (23.2 - 25)	73 - 75 (29.2 - 30)
Lung	102 (25.5)	77.5 (31)
Kidney (right)	99 - 104 (24.7 - 26)	73 - 78.5 (29.4 - 31.4)
(left)	103 - 108 (25.7 - 27)	75 - 80.5 (30.2 - 32.2)

Table 3. The table gives the descriptions of the two specimens of L. colubrina. Values for the position of organs are given as their distance from the snout of the specimen in centimetres with the corresponding distance in head lengths in brackets.

PARAMETER	MEAN	S.E.	RANGE	N
S.V. LENGTH (cm)				
Female	107.4	1.6	31.5 - 143.5	207
Male	72.7	1.2	27.5 - 97	150
TAIL LENGTH (cm)				
Female	11.7	0.2	3.0 - 16	204
Male	10.8	0.2	4.0 - 14.5	149
BLACK BANDS				
Female	28.8	0.1	23 - 34	189
Male	30.9	0.2	27 - 38	135
VENTRAL SCALES				
Female	228.6	0.4	222 - 238	81
Male	223.3	0.4	218 - 230	53
SUBCAUDAL SCALES				
Female	33.0	0.2	27 - 38	81
Male	41.6	0.2	37 - 46	55
WEIGHT (g)				
Female	622	21.9	15 - 1200	166
Male	173	8.6	17 - 393	95
UMBILICAL SCAR				
Female	203.1	0.56	197 - 209	33
Male	201.9	0.47	198 - 210	36
BODY SCALE ROWS				
(a) AT NECK				
Female	23	0.12	21 - 25	78
Male	22	0.06	21 - 23	48
(b) AT MID-BODY				
Female	23.8	0.02	23 - 25	84
Male	23	0.1	22 - 24	55
(c) AT VENT				
Female	20.1	0.08	18 - 22	77
Male	18.9	0.09	17 - 21	47
INFRALABIALS				
LHS & RHS				
Female	8.8	0.09	7 - 10	74
Male	8.3	0.1	7 - 10	42
SUPRALABIALS				
LHS & RHS				
Female	7.8	0.07	7 - 10	74
Male	7.0	0.03	7 - 8	42

Table 4. Morphological variation between females and males of _L. colubrina_. The statistics supplied are mean, standard error (S.E.), range and sample size (N).

	Median Test			ANOV		
Parameter	Chi²	dof	P	F	dof	P
Length	253.8	1	<.001	259.7	1,355	<.001
Tail Length	9.1	1	<.005	10.8	1,351	0.001
Black Bands	47.7	1	<.001	100.3	1,322	<.001
Ventrals	36.3	1	<.001	50.0	1,332	<.001
Subcaudals	106.5	1	<.001	635.1	1,134	<.001
Weight	145.1	1	<.001	230.2	1,259	<.001
Umbilical scar	1.1	1	>.25	2.5	1,67	0.114
Body Scale Rows						
(a) At Neck	2.4	1	>.1	59.8	1,124	<.001
(b) Mid-body	35.2	1	<.001	48.0	1,137	<.001
(c) Vent	11.0	1	<.001	87.5	1,122	<.001
Infralabials						
LHS	2.7	1	>.1	7.2	1,114	0.008
RHS	5.9	1	<.025	14.2	1,114	<.001
Supralabials						
LHS	41.9	1	<.001	52.9	1,114	<.001
RHS	40.3	1	<.001	55.2	1,114	<.001

Table 5. The significance of differences between males and females are shown as the Chi² value, degrees of freedom (dof) and probability (P) for the median test. F statistic, degees of freedom (dof) and probability (P) are given for Analysis of Variance (ANOV) for L. colubrina.

Position	Male	Female
Scale rows at neck	64% (31)	82% (34)
Intervening Ventrals	77% (31)	79% (34)
Scale rows at mid-body	94% (32)	76% (34)
Intervening ventrals	91% (32)	79% (34)
Scale rows at vent	75% (32)	62% (34)
Intervening ventrals	78% (32)	76% (34)

Table 6. Table presents the percentage of specimens which had an equal number of body scale rows when counted around the left and the right sides of the body. The number of specimens in the sample are given in brackets. The intervening ventral scales are presented in the same manner.

Position	Male	Female
Scale rows at neck	21 (37%) & 23 (40%)	23 (83%)
Scale rows at mid-body	23 (96%)	23 (49%)
scale rows at vent	19 (81%)	20 (77%)

Table 7. The table presents the modal count and percentage of the sample having that count of body scale rows for males and female _L. colubrina_.

	L. colubrina		*L. s. schistorhynchus*		COMBINED *L. colubrina* & *schistorhynchus*	
	Male	Female	Male	Female	Male	Female
At Neck						
b	.45	.55	.57	.25	.48	.46
a	1.68	-.53	-1.09	6.3	1.02	1.54
r	.73	.66	.83	.56	.79	.63
N	46	78	26	5	72	83
At Mid-body						
b	.5	.56	.49	*	.48	.56
a	.5	-1	.77	*	.99	-.95
r	.5	.74	.96	*	.89	.75
N	47	77	26	5	73	82
At Vent						
b	.33	.45	.51	.5	.35	.41
a	3.87	1.2	.8	.6	3.46	1.99
r	.45	.56	.79	.65	.7	.61
N	47	77	26	5	73	82

Table 8. The table gives the values to evaluate the equation of $y = bx + a$ where y is the number of ventral scales that correspond to a count of body scale rows (x) around the species indicated. The correlation coefficient (r) is given as is the number in the sample (N). The values are for *L. colubrina*, *L. s. schistorhynchus*, and for those of these species combined. The values could not be calculated for those shown by the asterisk (*) as all the points were identical thereby giving neither regression nor correlation values.

	Male	Female
Infralabials		
Left side / Right side	8 / 8	9 / 9
% of sample	52% / 57%	46% / 50%
Supralabials		
Left side / Right side	7 / 7	8 / 8
% of sample	95% / 98%	53% / 56%
N	42	74

Table 9. The table gives the mode and corresponding percentage of male amd female specimens for the number of infralabial and supralabial scales on the left side and right side of the mouth. The sample size (N) is also given.

VARIABLES		MALES				FEMALES			
Independent / Dependent	b	a	r	(N)	b	a	r	(N
s-v length / subcaudals	.02	40.3	.18	(55)	.02	30.5	.28	(8
s-v length / ventrals	.02	221.8	.13	(53)	.05	222.7	.35	(8
s-v length / bands	-.01	31.6	.06	(135)	.01	27.4	.17	(1
s-v length / tail l.	.17	-1.4	.96	(149)	.1	.9	.95	(2
s-v length / weight	4.8	-169.5	.93	(95)	10.3	-482.8	.84	(1
tail l. / subcaudals	.15	40.0	.25	(55)	.34	29.2	.44	(8
ventrals / bands	.11	6.7	.17	(53)	.13	-.06	.25	(8

Table 10. Relationship between selected morphometric variables for male and female _L. colubrina_. Table gives the values to evaluate the equation $y = bx + a$; correlation coefficient (r) by least squares, where y is the dependent variable and x is the independent variable. Sample size is given by N in brackets. Figure 5 (e) revealed that the relationship between s-v length and weight was non-linear and the equations, $y = 0.42x^3$, $r = 0.94$ for males, and $y = 0.44x^3 + 0.02$, $r = 0.87$ for females, are more appropriate.

CLASSES	SIZE	PHASE OF MATURATION
Follicles	(mm)	(after Zug *et al.* 1979)
I	< 1.0	oogenesis
II	1.1 - 5.0	early growth
III	5.1 - 8.0	hydration and initial vitellogenesis
IV	8.1 - 15.0	active vitellogenesis
V	15.1 >	maturation to ovulation
Eggs	42.1 >	oviducal and shell formation

Table 11. Size classes of ovarian follicles and shelled oviducal eggs for *L. colubrina.* The measurements are in millimetres, and the choice of size classes is based on the lower frequencies of follicle diameter of 68 specimens.

PARAMETER	CLUTCH NUMBER 1	2	3	4	5
Egg Length (cm)					
mean	6.8	7.0	6.3	6.8	6.2
s.e.	.09	.24	.14	.16	.15
minimum	6.4	5.5	5.6	6.1	5.4
maximum	7.2	8.2	6.7	7.4	6.6
Egg Width (cm)					
mean	2.7	2.4	2.9	2.8	2.6
s.e.	.11	.06	.03	.09	.09
minimum	2.5	2.0	2.8	2.2	2.1
maximum	2.9	2.8	3.1	3.0	2.8
Egg Weight (g)					
mean	24.3	21.1	32.6	29.0	20.3
s.e.	.3	1.01	.29	.43	1.04
minimum	22.5	13.0	31.4	27.1	13.9
maximum	26.0	24.5	33.4	30.7	22.6
Clutch Size					
N	10	10	7	7	7

Table 12. The table gives the mean, standard error (s.e.) and range of the egg length, egg width and weight plus the number of eggs in five clutches laid in captivity by different specimens of _L. colubrina_.

	Egg Number	
	#3	#6
Weight at Laying (g)	33.4	33.5
Egg Length (cm)	5.9	6.5
Weight at Hatching (g)	36.6	34.3
Incubation Period	126 days	121 days
Weight of Snake (g)	23.8	17.3
S-v length at birth (cm)	30.7	27.5
Sex	male	male
Incubation Temperatures	24°C to 32.5°C	

Table 13. The table gives the weights and lengths of the eggs and hatchlings of two successful eggs from a clutch of seven laid by a captive female *L. colubrina* on 9 December 1981.

Hemipenis Parameter	Mean	s.e.	Range	N
Tip to Tip Distance (cm)	0.93	.03	.35 - 1.26	33
Spinous Length (cm)	1.10	.02	.8 - 1.33	33
Calyculate Length (cm)	1.12	.02	.6 - 1.3	33
Maximum Diameter (cm)	1.37	.03	.65 - 1.66	33

Table 14. The table presents the mean, standard error (s.e.) and range of measurements of hemipenes for 33 male L. colubrina. The left and right hemipenis were inflated with water to full extension and measured. The averages of these provided the data for the calculations.

FAMILY: MURAENESOCIDAE

Conger cinereus *

Lycodontis pictus

FAMILY: MURAENIDAE

Gymnothorax tessellatus *

Gymnothorax meleagris

Gymnothorax favagineus

Gymnothorax buroensis

Echidna nebulosa *

Uropterygius tigrinus

Siderea picta

Table 15. Table lists the species of eel found in the stomachs of *L. colubrina*. The most common species are indicated by an asterisk (*).

Study Area

Date	1			2			3			4			5			6			7			8			9			TOTAL		
	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J
8.02.81	-	-	-	37	15	0	6	3	1	1	2	1	27	30	1	-	-	-	-	-	-	-	-	-	-	-	-	71	50	3
21 to 24.04.81	-	-	-	63	62	1	14	7	0	16	14	0	52	45	1	-	-	-	7	0	0	-	-	-	-	-	-	152	128	2
9 to 12.07.81	15	8	1	64	56	3	22	26	1	1	1	0	1	2	1	-	-	-	1	0	2	13	4	31	-	-	-	117	87	39
5 to 12.01.81	4	2	0	117	62	0	11	6	0	7	5	0	207	137	0	-	-	-	3	0	2	20	10	2	-	-	-	369	222	4

Table 16. Table presents the total number of _L. colubrina_ caught on Sausau Island for each visit and for each study area of the island. Numbers are presented for males (M), females (F) and juveniles (J) for each study area (1 to 9). See text for descriptions of the areas and refer to Figure 16.

		Expected Frequencies		
Number of captures	Number of individuals	Poisson	Negative binomial	Geometric
1	145	143.76	179.94	145.15
2	24	25.86	29.26	23.37
3	3	3.10	4.57	3.76
4	1	.28	.70	.61
Chi Square		2.01	8.40	.43
Degrees of Freedom		2	1	2
Probability		0.5	<0.001	0.75
Estimate of N		573	971	1075*

Table 17 (a). Table gives the zero-truncated Poisson, negative binomial and geometric distributions fitted to capture frequencies of _L. colubrina_ on Sausau Island in April 1981. The best estimate of the population size is indicated by an asterisk (*).

Number of captures	Number of individuals	Expected Frequencies: Poisson	Negative binomial	Geometric
1	109	108.21	41.45	108.54
2	11	12.76	4.36	11.97
3	2	1.00	.53	1.32
4	0	.06	.07	.15
Chi Square		1.29	124.30	.58
Degrees of Freedom		2	1	2
Probability		0.5	<0.001	0.75
Estimate of N		581	2130	1106*

Table 17 (b). Table gives the zero-truncated Poisson, negative binomial and geometric distributions fitted to capture frequencies of L. colubrina on Sausau Island in July 1981. The best estimate of the population size is indicated by an asterisk (*).

		Expected Frequencies		
Number of captures	Number of individuals	Poisson	Negative binomial	Geometric
1	378	376.73	3002.32	381.58
2	73	76.01	589.41	67.77
3	12	10.22	84.63	12.04
4	1	1.03	9.92	2.14
5	0	0.08	1.01	0.38
Chi Square		0.51	2817.73	1.42
Degrees of Freedom		3	2	3
Probability		0.9	<0.001	0.75
Estimate of N		1398*	1530	2612

Table 17 (c). Table gives the zero truncated Poisson, negative binomial and geometric distributions fitted to capture frequencies of L. colubrina on Sausau Island in January 1982. The best estimate of the population size is indicated by an asterisk (*).

In Water

	Body Temperature	Water Temperature	Difference in Temperatures
Mean	29.0	29.3	Body temperatures ranged
S.E.	0.4	0.4	from 1°C above to 1.5°C
Minimum	24.0	24.0	below water temperature.
Maximum	32.0	32.5	
N	31	31	

Moving on Land

	Body Temperature	Air Temperature	Difference in Temperatures
Mean	27.1	26.3	Body temperatures ranged
S.E.	0.3	0.3	from 6.5°C above to 2°C
Minimum	21.0	20.5	below air temperature.
Maximum	32.0	30.0	
N	63	63	

Resting on Land

	Body Temperature	Ground Temperature	Difference in Temperatures
Mean	27.1	26.1	Body temperatures ranged
S.E.	0.2	0.2	from 5°C above to 1.5°C
Minimum	24.5	23.5	below ground temperature.
Maximum	30.5	29.0	
N	67	67	

Resting on Land

	Body Temperature	Air Temperature	Difference in Temperatures
Mean	27.5	26.9	Body temperatures ranged
S.E.	0.1	0.1	from 7°C above to 2.5°C
Minimum	24.0	23.0	below air temperature.
Maximum	31.0	31.0	
N	146	146	

Table 18. The table presents the mean, standard error (S.E.) and ranges of temperatures recorded for L. colubrina and the immediate environment. The body temperatures were recorded for snakes in water, and on land and for resting or moving individuals as indicated. The maximum differences between environmental temperatures and cloacal temperatures are presented in each instance.

	Animal		Venom Yield			
Sex	S-V L (cm)	Wt. (g)	Wet Wt. (mg)	Volume (µl)	Dry Wt. (mg)	% Solid
M	76	200	18.1	12.3	5.8	32.0
M	79.5	150	9.4	6.6	2.8	29.8
F	105	450	40.6	26.4	14.2	35.0
F	125.5	600	21.3	14.8	6.5	30.5
F	114	900	43.3	31.6	11.7	27.0
F	118	1050	114.4	78.7	35.7	31.2
F	109	700	21.1	15.5	5.6	26.5
F	127.5	800	29.3*	20.0	9.3	31.7
F	107	550	9.1	5.3	3.8	41.8
Mean =	106.8	600	34.1	23.5	10.6	31.7
S.E. =	6.1	100	10.8	7.5	3.4	1.6

* This represents the venom from one fang. The other was dislodged during collection and its venom lost.

Table 19. Results of venom extraction from Group I animals (water supplied) on (September 1, 1981). The animals were collected eight days prior to venom extraction. See text for details.

Animal			Venom Yield			
Sex	SVL (cm)	Wt. (g)	Wet Wt. (mg)	Volume (µl)	Dry Wt. (mg)	% Solid
M	90	250	32.5	23.3	9.2	28.3
F	104	600	48.7	33.2	15.5	31.8
F	120	750	20.2	14.4	5.8	28.7
F	129	1200	42.8	30.1	12.7	29.7
F	121	850	84.9	59.6	25.3	29.8
F	118.5	800	86.3	60.3	26.0	30.1
F	119.5	950	64.2	45.7	18.5	28.8
F	113	750	16.1	11.2	4.9	30.4
Mean =	114.3	769	49.5	34.7	14.7	29.7
S.E. =	4.3	97	9.6	6.7	2.9	0.4

Table 20. Results of venom extraction from Group II animals (water deprived) on (September 1, 1981). The animals were collected eight days prior to venom extraction. See text for details.

FIGURES

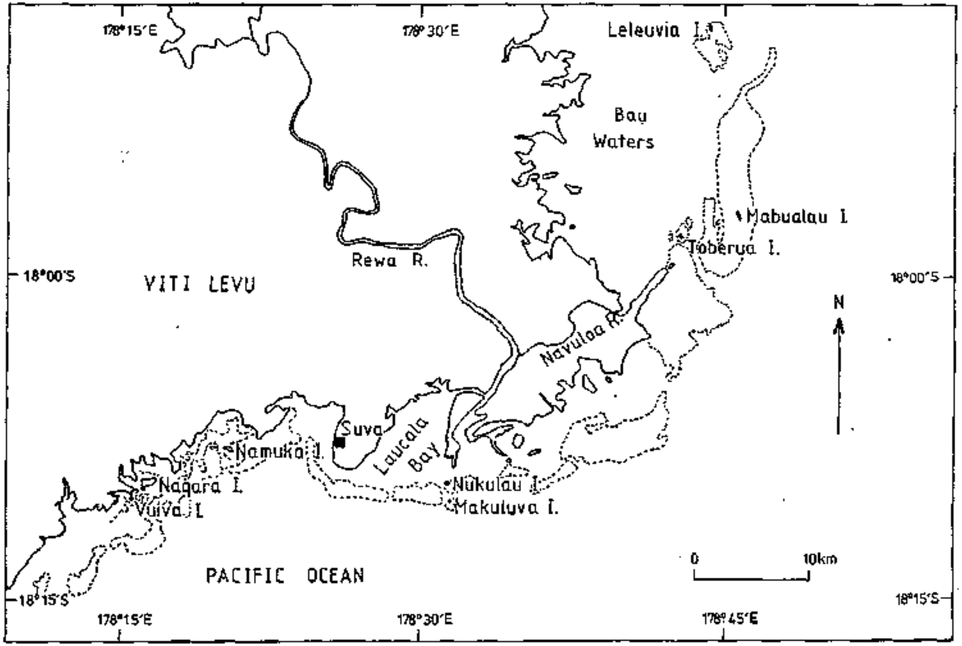


Figure 1. The study areas for L. colubrina in South East Viti Levu.

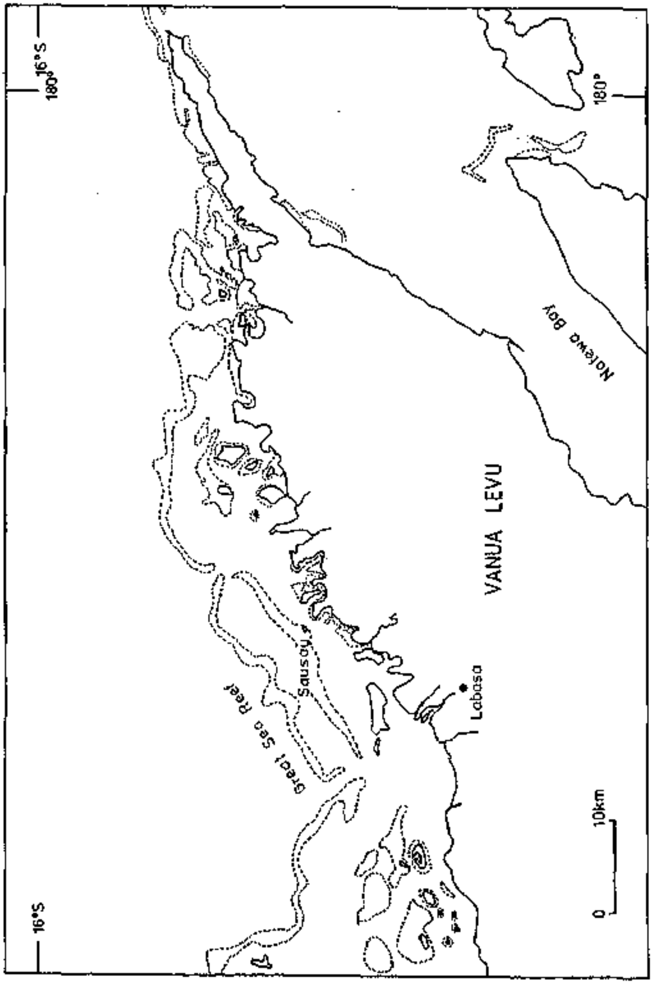


Figure 2. The study area for <u>L. colubrina</u> north of Vanua Levu showing Sausau Island.

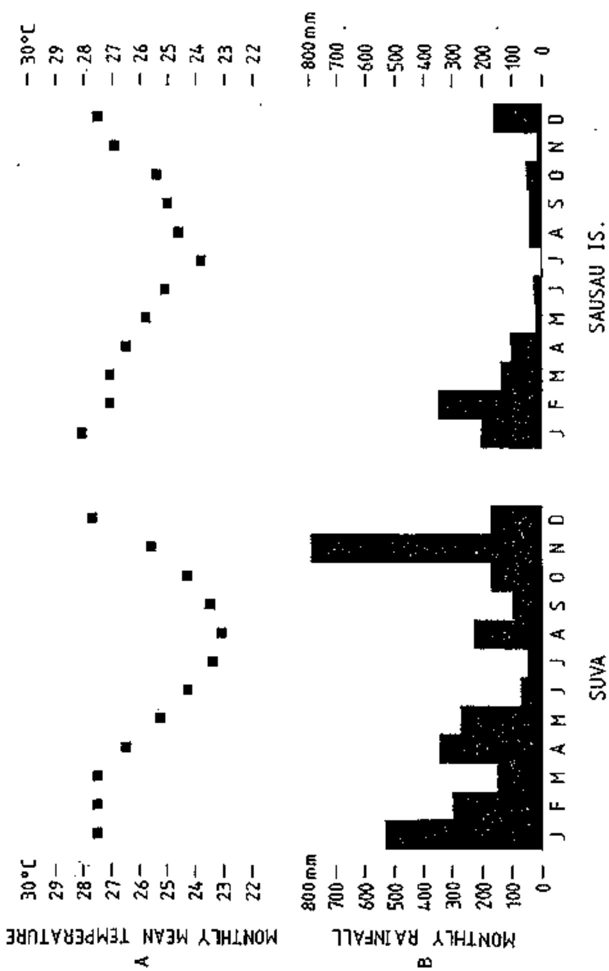


Figure 3. The monthly mean temperature (A) and monthly rainfall (B) fo South East Viti Levu (Suva) and for Vavalagi 6km south of Sausau Island Vanua Levu for 1981.

Figure 4(a - l). Comparisons between male and female L. colubrina are shown for the parameters measured. The figures show the frequency of a count or measurement as a bar graph with that of males on the left-hand side and females on the right. Where the frequency exceeds 40 for either males or females, the total for the sex is given at the end of the bar. The number of specimens of each sex making up the sample is shown as (N) on the left for males and on the right for females. The size classes (with units) or counts are presented in the central column. The parameters are: (a) s.v. length (cm), (b) tail length (cm), (c) number of black bands, (d) number of ventral scales, (e) number of subcaudal scales, (f) weight (g), (g) ventral scale number of umbilicus, (h) number of body scale rows at neck, (i) at midbody, (j) at vent, (k) number of infralabial scales, (l) number of supralabial scales.

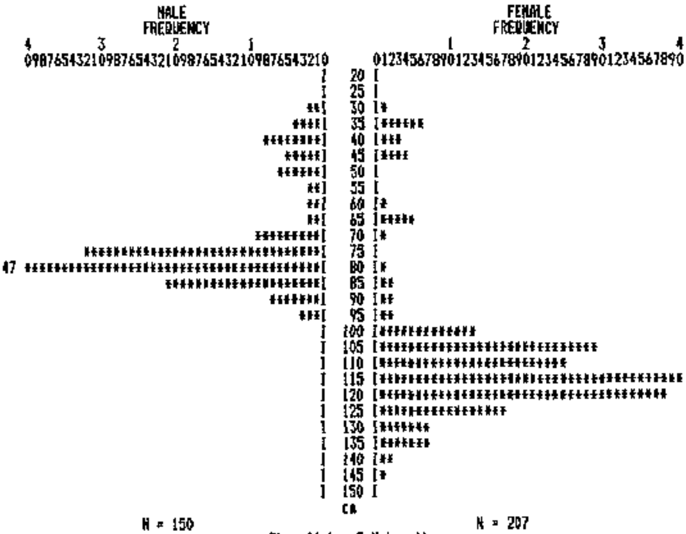


Fig. 4(a). S-V Length

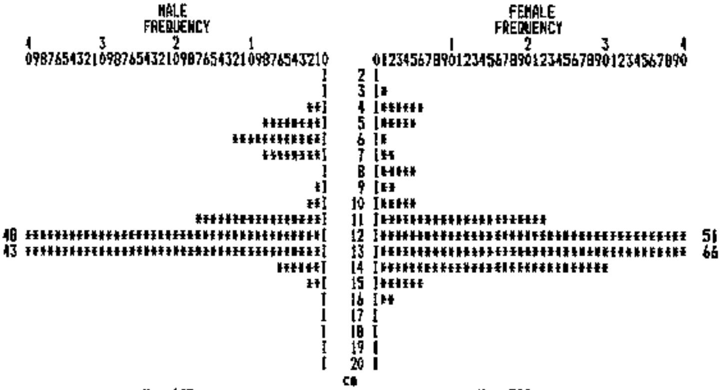


Fig. 4(b). Tail Length

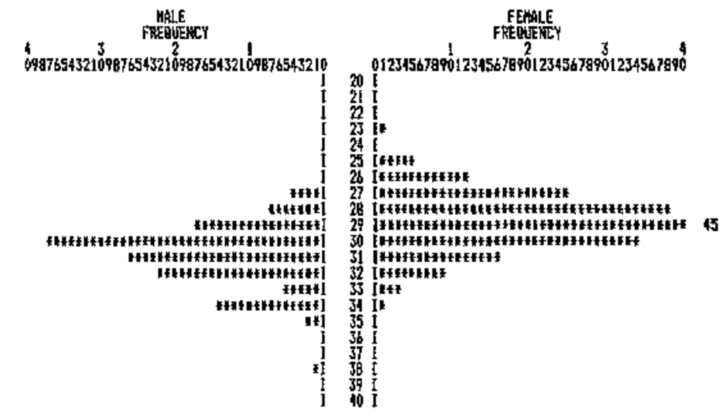


Fig. 4(c). Number of Black Bands

```
                  MALE                                                        FEMALE
                FREQUENCY                                                   FREQUENCY
4         3         2         1                                 1         2         3         4
09876543210987654321098765432109876543210      01234567890123456789012345678901234567890
                                        I  215 I
                                        I  216 I
                                        I  217 I
                                      **I  218 I
                                       *I  219 I
                                   *****I  220 I
                                  ******I  221 I
                              **********I  222 I**
                                  ******I  223 I****
                                  ******I  224 I****
                                  ******I  225 I****
                                    ****I  226 I**********
                                      **I  227 I*********
                                      **I  228 I*********
                                       *I  229 I******
                                      **I  230 I************
                                        I  231 I******
                                        I  232 I*****
                                        I  233 I****
                                        I  234 I*
                                        I  235 I*
                                        I  236 I**
                                        I  237 I*
                                        I  238 I*
                                        I  239 I
                                        I  240 I

               N = 53                                          N = 81
```

Fig. 4(d). Number of Ventral Scales

```
                  MALE                                                        FEMALE
                FREQUENCY                                                   FREQUENCY
4         3         2         1                                 1         2         3         4
09876543210987654321098765432109876543210      01234567890123456789012345678901234567890
                                        I   25 I
                                        I   26 I
                                        I   27 I*
                                        I   28 I*
                                        I   29 I**
                                        I   30 I****
                                        I   31 I**********
                                        I   32 I***********
                                        I   33 I******************
                                        I   34 I***************
                                        I   35 I************
                                        I   36 I****
                                       *I   37 I*
                                        I   38 I**
                                   *****I   39 I
                                 *******I   40 I
                         ***************I   41 I
                             ***********I   42 I
                             ***********I   43 I
                                     ***I   44 I
                                        I   45 I
                                      **I   46 I
                                        I   47 I
                                        I   48 I
                                        I   49 I
                                        I   50 I

               N = 55                                          N = 81
```

Fig. 4(e). Number of Subcaudal Scales

```
                MALE                                                FEMALE
              FREQUENCY                                           FREQUENCY
4         3         2         1                                 1         2         3         4
09876543210987654321098765432109876543210      0123456789012345678901234567890123456789O
                                  *******I     0 I******
                            *************I    50 I*****
                                       **I   100 I****
                               **********I   150 I***
      ***********************************I   200 I**
                  ***********************I   250 I**
                                     ****I   300 I**
                                         I   350 I**
                                        *I   400 I*******
                                         I   450 I**********
                                         I   500 I**********
                                         I   550 I***********
                                         I   600 I**************
                                         I   650 I***********
                                         I   700 I**************
                                         I   750 I*********
                                         I   800 I****************
                                         I   850 I*********
                                         I   900 I*******
                                         I   950 I*********
                                         I  1000 I****
                                         I  1050 I****
                                         I  1100 I*
                                         I  1150 I
                                         I  1200 I****
                                              g
             N = 95                                            N = 166
```

Fig. 4(f). Body Weight

```
                MALE                                                FEMALE
              FREQUENCY                                           FREQUENCY
4         3         2         1                                 1         2         3         4
09876543210987654321098765432109876543210      01234567890123456789012345678901234567890
                                         I   195 I
                                         I   196 I
                                         I   197 I**
                                     ****I   198 I*
                                      ***I   199 I
                                    *****I   200 I***
                                   ******I   201 I*****
                                    *****I   202 I*****
                                      ***I   203 I***
                                      ***I   204 I**
                                      ***I   205 I*****
                                        *I   206 I
                                       **I   207 I**
                                         I   208 I****
                                         I   209 I*
                                        *I   210 I

             N = 36                                            N = 33
```

Fig. 4(g). Umbilicus Position from the First Ventral Scale

```
                    MALE                                               FEMALE
                  FREQUENCY                                          FREQUENCY
   4         3         2         1                             1         2         3         4
   09876543210987654321098765432109876543210       01234567890123456789012345678901234567890
                                           I   20 I
                         ******************I   21 I*
                                ***********I   22 I******
                        *******************I   23 I****************************************  65
                                           I   24 I****
                                           I   25 I**
                                           I   26 I
                                           I   27 I
                                           I   28 I
                                           I   29 I
                                           I   30 I

                  N = 48                                             N = 78
```

Fig. 4(h). Number of Scale Rows at Neck

```
                    MALE                                               FEMALE
                  FREQUENCY                                          FREQUENCY
   4         3         2         1                             1         2         3         4
   09876543210987654321098765432109876543210       01234567890123456789012345678901234567890
                                           I   20 I
                                           I   21 I
                                          *I   22 I
53 ****************************************I   23 I****************************************  41
                                          *I   24 I*************
                                           I   25 I******************************
                                           I   26 I
                                           I   27 I
                                           I   28 I
                                           I   29 I
                                           I   30 I

                  N = 55                                             N = 84
```

Fig. 4(i). Number of Scale Rows at Mid-Body

```
                    MALE                                               FEMALE
                  FREQUENCY                                          FREQUENCY
   4         3         2         1                             1         2         3         4
   09876543210987654321098765432109876543210       01234567890123456789012345678901234567890
                                           I   15 I
                                           I   16 I
                                         **I   17 I
                                       ****I   18 I*
      *************************************I   19 I***********
                                        ***I   20 I****************************************  44
                                          *I   21 I********************
                                           I   22 I*
                                           I   23 I
                                           I   24 I
                                           I   25 I

                  N = 47                                             N = 77
```

Fig. 4(j). Number of Scale Rows at Vent

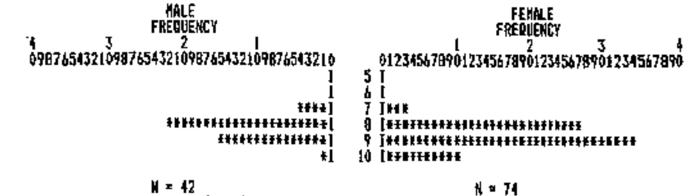


Fig. 4(k.1). Left Infralabial Scale Count

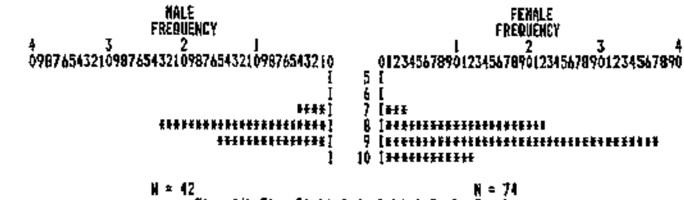


Fig. 4(k.2). Right Infralabial Scale Count

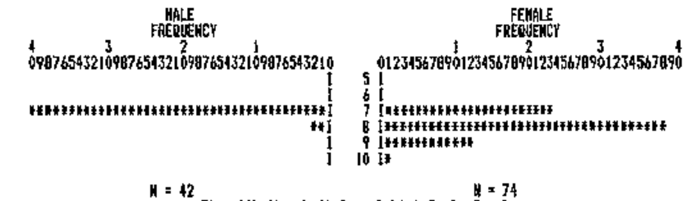


Fig. 4(l.1). Left Supralabial Scale Count

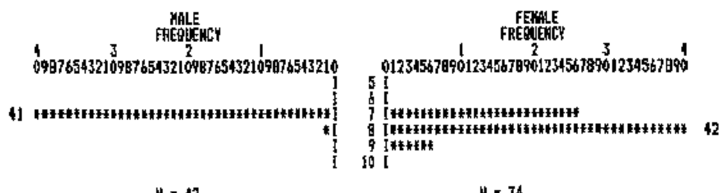


Fig. 4(l.2). Right Supralabial Scale Count

Figure 5 (a - g). Graphs of selected morphological characters are presented for each sex to illustrate their relationship, if any. The graphs are as follows;

(a) s-v length (cm) and subcaudal scale count for males (upper) and females (lower).

(b) s-v length (cm) and ventral scale count for males (upper) and females (lower).

(c) s-v length (cm) and black band count for males (upper) and females (lower).

(d) s-v length (cm) and tail length (cm) for males (upper) and females (lower).

(e) s-v length (cm) and weight (g) for males (upper) and females (lower).

(f) tail length (cm) and subcaudal scales for males (upper) and females (lower).

(g) number of ventral scales and number of bands for males (upper) and females (lower).

The sex, regression equation, correlation coefficient (r) and sample size (n) are given for each graph.

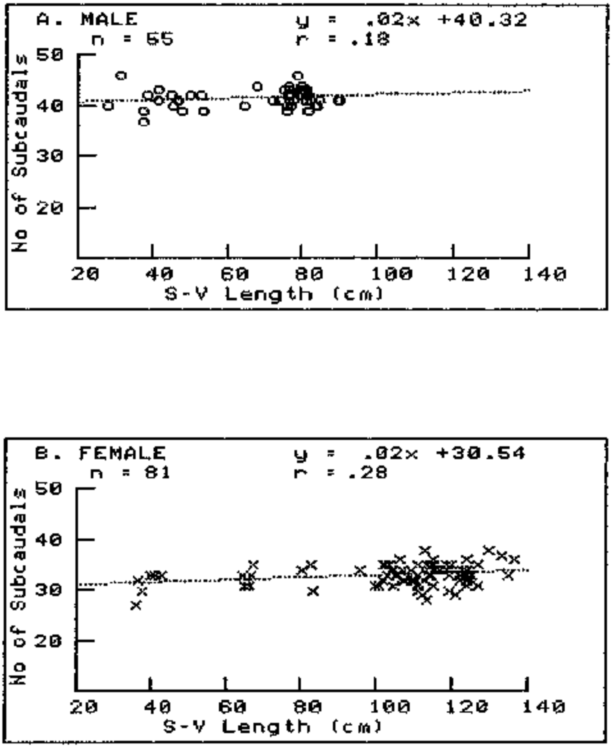
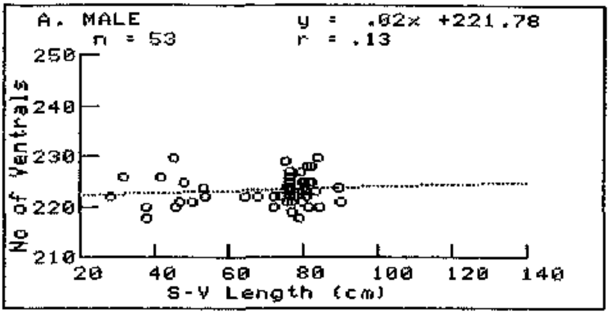

A. MALE
n = 55
y = .02x +40.32
r = .18
No of Subcaudals
50
40
30
20
20
40
60
80
100
120
140
S-V Length (cm)
B. FEMALE
n = 81
y = .02x +30.54
r = .28
No of Subcaudals
50
40
30
20
20
40
60
80
100
120
140
S-V Length (cm)

Figure 5(a)


A. MALE
n = 53
y = .02x +221.78
r = .13
No of Ventrals
250
240
230
220
210
20
40
60
80
100
120
140
S-V Length (cm)

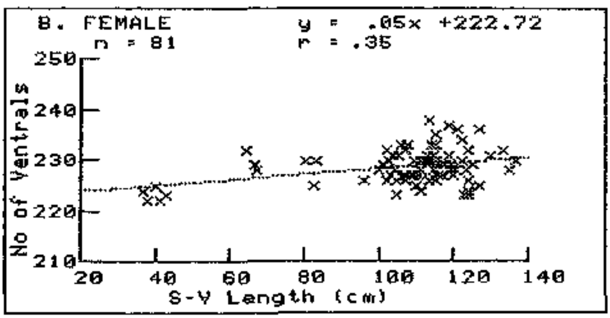

B. FEMALE
n = 81
y = .05x +222.72
r = .35
No of Ventrals
250
240
230
220
210
20
40
60
80
100
120
140
S-V Length (cm)

Figure 5(b)

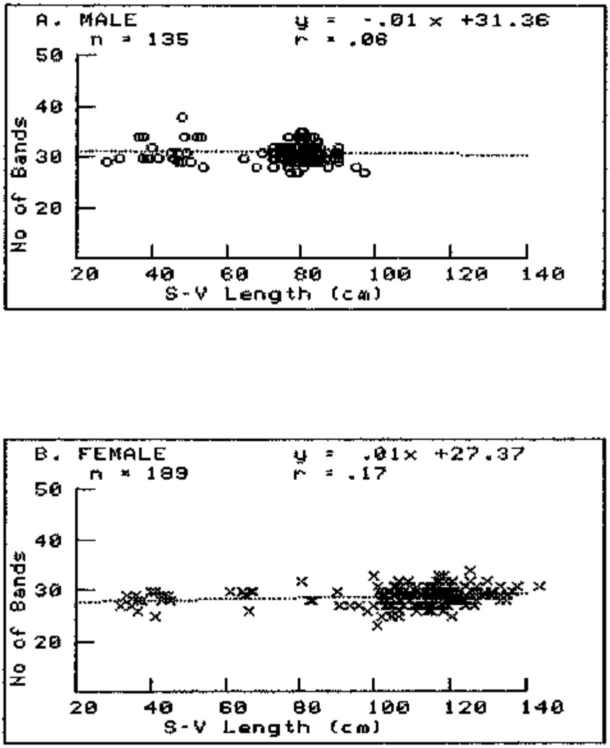
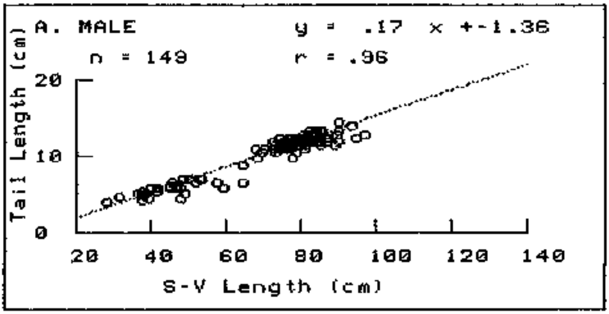

A. MALE
n = 135
y = -.01 x +31.36
r = .06
No of Bands
S-V Length (cm)
B. FEMALE
n = 189
y = .01x +27.37
r = .17
No of Bands
S-V Length (cm)

Figure 5(c)


A. MALE
y = .17 x +-1.36
n = 149
r = .96
Tail Length (cm)
0
10
20
20
40
60
80
100
120
140
S-V Length (cm)

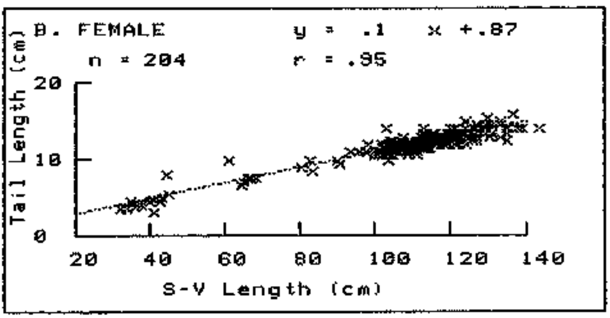

B. FEMALE
y = .1 x +.87
n = 204
r = .95
Tail Length (cm)
0
10
20
20
40
60
80
100
120
140
S-V Length (cm)

Figure 5(d)

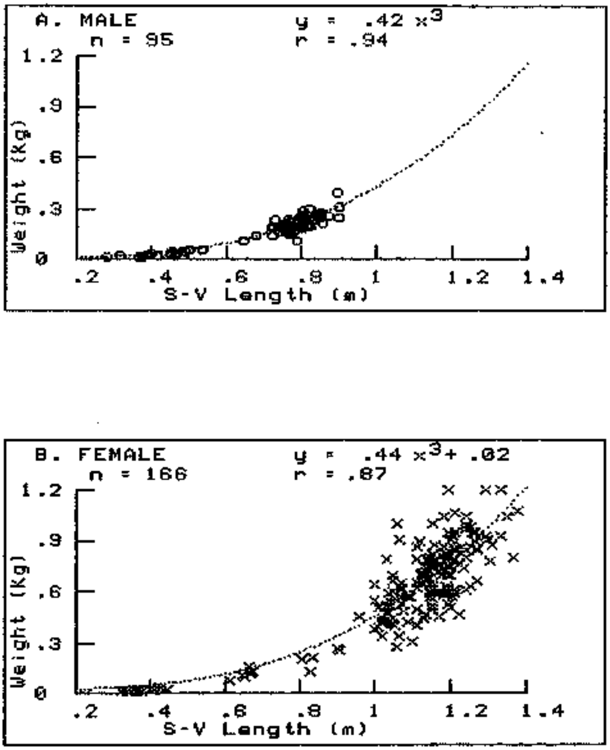

A. MALE
n = 95
y = .42 x^3
r = .94
Weight (Kg)
1.2
.9
.6
.3
0
.2
.4
.6
.8
1
1.2
1.4
S-V Length (m)
B. FEMALE
n = 166
y = .44 x^3 + .02
r = .87
Weight (Kg)
1.2
.9
.6
.3
0
.2
.4
.6
.8
1
1.2
1.4
S-V Length (m)

Figure 5(e)

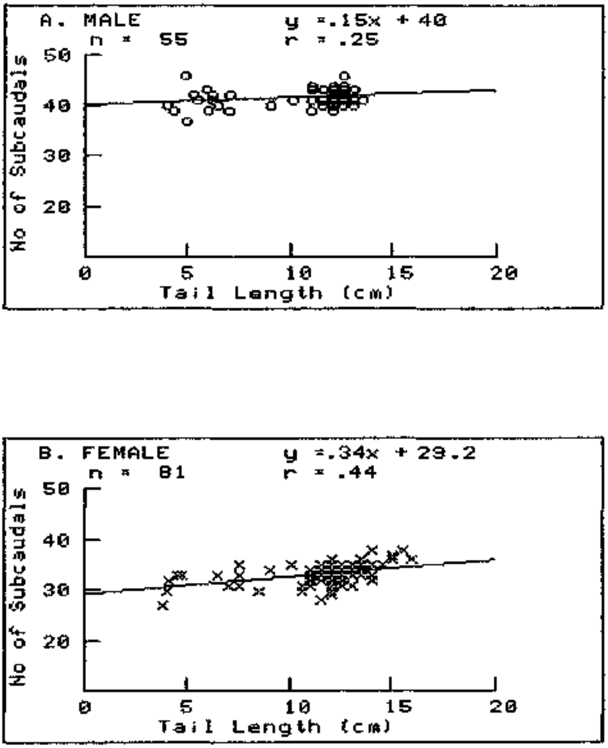

A. MALE
n = 55
y =.15x + 40
r = .25
No of Subcaudals
50
40
30
20
0
5
10
15
20
Tail Length (cm)
B. FEMALE
n = 81
y =.34x + 29.2
r = .44
No of Subcaudals
50
40
30
20
0
5
10
15
20
Tail Length (cm)

Figure 5(f)

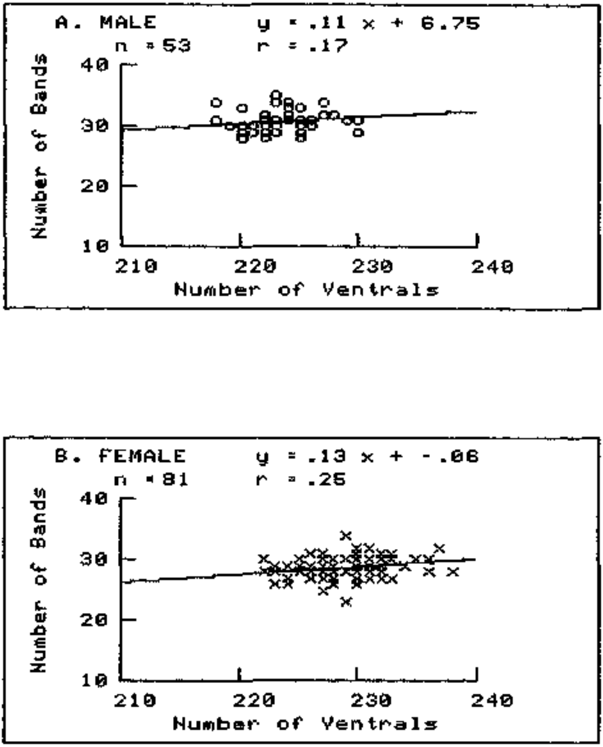

A. MALE
y = .11 x + 6.75
n = 53
r = .17
Number of Bands
40
30
20
10
210
220
230
240
Number of Ventrals
B. FEMALE
y = .13 x + -.06
n = 81
r = .26
Number of Bands
40
30
20
10
210
220
230
240
Number of Ventrals

Figure 6. The relationships between the number of ventral scales and the number of black bands are presented for three species of _Laticauda_ (a) and _Hydrophis melanocephalus_ (b). The means and ranges are shown for the numbers of bands and ventral scales. The mean for each population from the North Pacific and South Pacific are joined by an oblique line for each species. Males were used in most cases although some authors did not differentiate between males and females when they presented the variation in band count e.g. Mao and Chen (1980). In such instances, the average of their ranges was used. The species are;

(a)

1. _L. s. schistorhynchus_ from Niue (Guinea _et al._, 1983).
2. _L. semifasciata_ from Ryu Kyu Islands (Guinea _et al._, 1983).
3. _L. colubrina_ from Fiji (this study).
4. _L. colubrina_ from Taiwan (Mao and Chen, 1980).
5. _L. laticaudata_ from New Caledonia (Saint Girons, 1964).
6. _L. laticaudata_ from Taiwan (Mao and Chen, 1980).

(b)

7. _Hydrophis melanocephalus_ from Fiji (Guinea, 1981).
8. _H. melanocephalus_ from Taiwan (Mao and Chen, 1980).

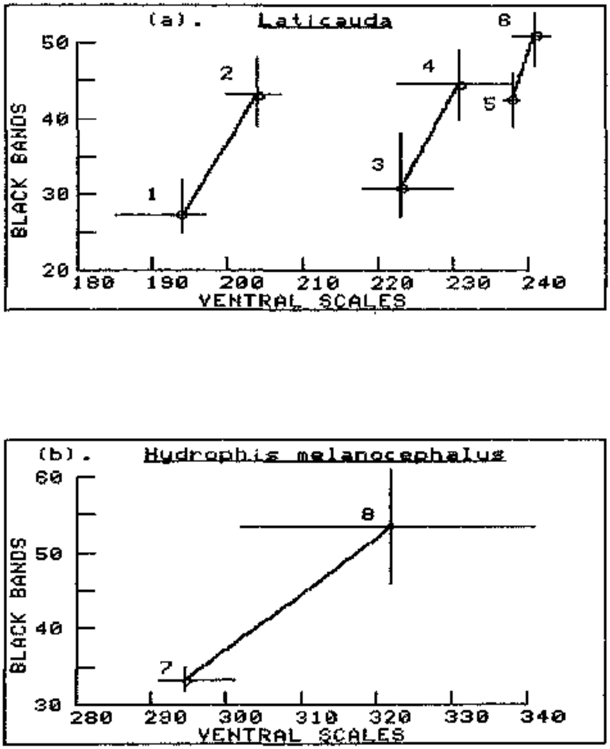

(a). Laticauda
BLACK BANDS
20
30
40
50
180
190
200
210
220
230
240
VENTRAL SCALES
1
2
3
4
5
6
(b). Hydrophis melanocephalus
BLACK BANDS
30
40
50
60
280
290
300
310
320
330
340
VENTRAL SCALES
7
8

Figure 6.

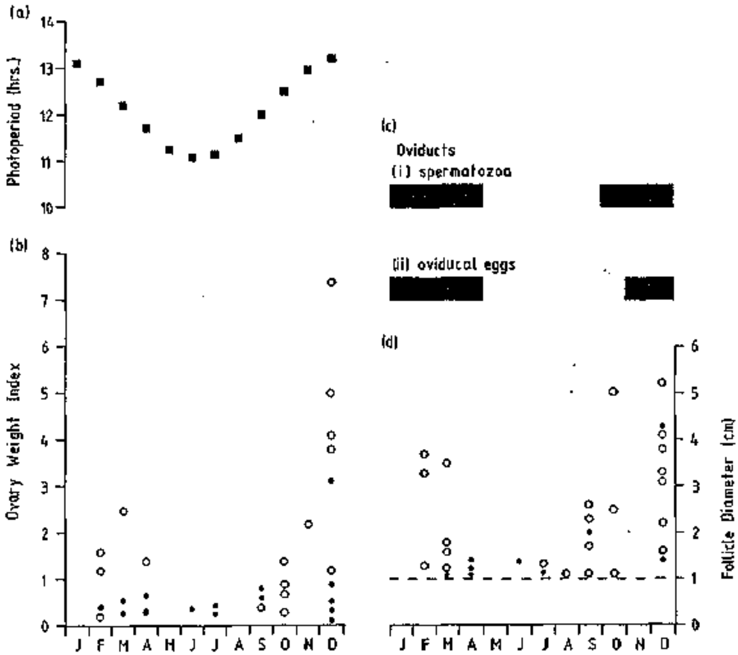


Figure 7. This figure presents the monthly variation in (a) photoperiod, (b) ovary weight index, (c) the presence of spermatozoa (i) and oviducal eggs (ii) in the oviducts and (d) the diameter of the largest follicle present in the ovaries of the 68 adult female L. colubrina dissected during the study. Solid circles represent multiple points.

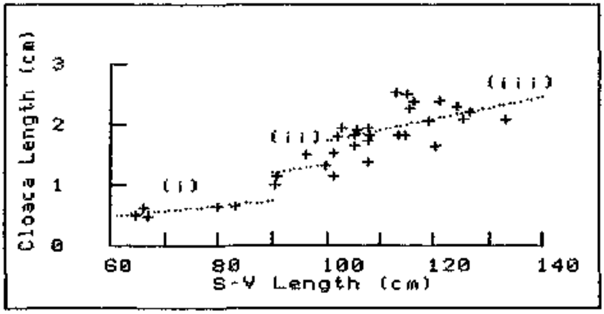


Figure 8. The length of the cloaca obtained from silicone moulds of females fall within three classes. Those females whose s-v length is below 90 cm are immature. Maturity occurs when s-v length falls between 90 and 100 cm. Those specimens over 100 cm are adult. There is a slight increase in cloacal length with s-v length and presumably with the age of the snake. The regression equations for the three sections of the graph are;

(i) [s-v length < 90 cm] $y = 0.008x + 0.003$, $r = 0.98$.

(ii) [s-v length 90 - 100 cm] $y = 0.014x - 0.015$, $r = 0.96$.

(iii) [s-v length > 100 cm] $y = 0.018x - 0.078$, $r = 0.84$.

where y is the length of the cloacal mould, x is the s-v length, and r is the correlation coefficient.

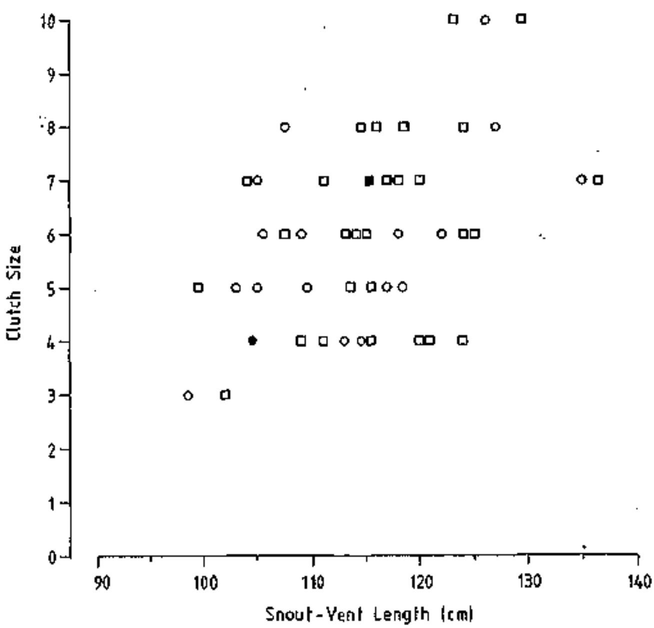


Figure 9. The graph presents the relationship between maternal s-v length and the number of eggs in a clutch for L. colubrina. Circles represent oviducal eggs and clutches laid in captivity. Squares represent the count made by palpation of live females. Solid symbols represent multiple scores.

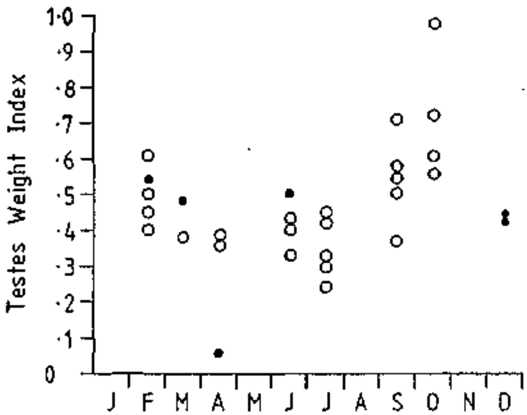
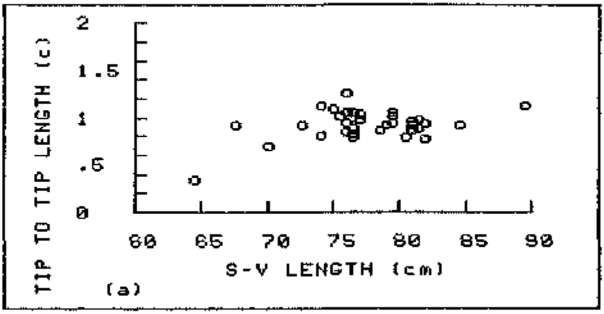


Figure 10. The variation in testes weight index is shown for each month of the study. The testes weight index was at its miniaum during the winter months, April to July, and at its maximum in September and October. Open circles show values. Solid circles show multiple values.

Figure 11. The size of male *L. colubrina* at sexual maturity is determined by the variation of hemipenis parameters with the s-v length of the specimen. The straight line distance from the distal terminals of the sulcus spermaticus (a), the length of the hemipenis covered with calyces (b), the length of the hemipenis supporting spines (c) and the maximum diameter (d) are plotted against the s-v lenght of the specimen. Adult dimensions of all parameters were present after the specimens had obtained a length of 70 cm. This size was taken to be the size at sexual maturity.



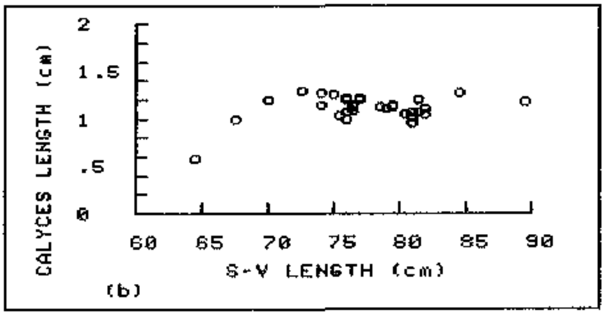
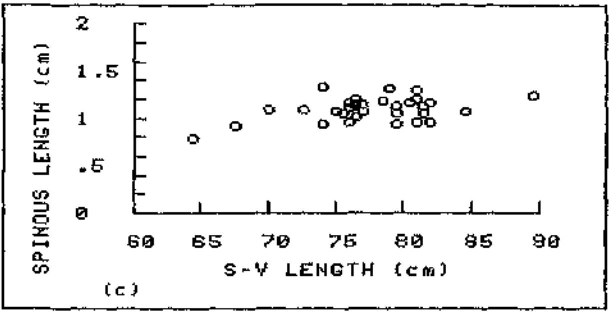


Figure 11(a) upper; Figure 11(b) lower



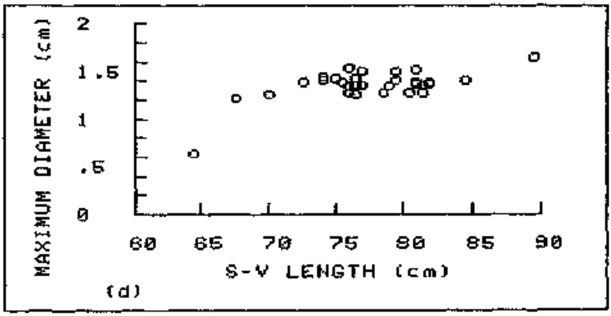


Figure 11(c) upper; Figure 11(d) lower

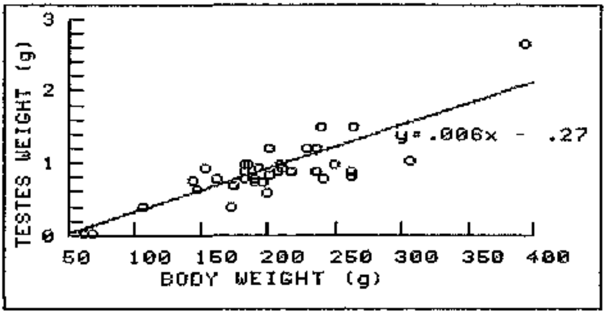


Figure 12 The weight of the testes is directly proportional to body weight of male L. colubrina. Both weights are expressed in grams. The regression equation is displayed on the figure. The sample size is 36 and the correlation coefficient equals 0.78.

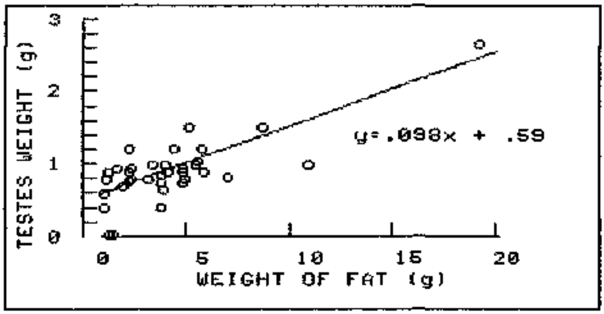


Figure 13. Testes weight is directly proportional to the weight of fat in the body of male L. colubrina. Both weights are given in grams. The regression equation is presented on the figure. The sample size is 36 and the correlation coefficient equals 0.87.

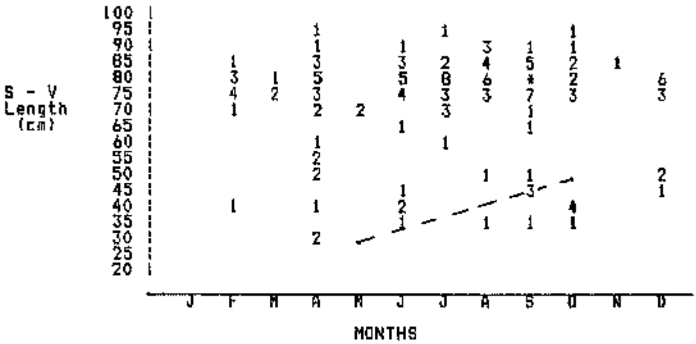


Figure 14 (a) Body size - month matrix showing the seasonal distribution in s-v length according to the month of collection for all male L. colubrina caught on the islands of S. E. Viti Levu. Sample size = 150. The inferred juvenile growth rate is shown as a broken line. (Numbers = individuals of a given s-v length class caught in a specific month. * indicates more than 10 specimens in the class for that month.)

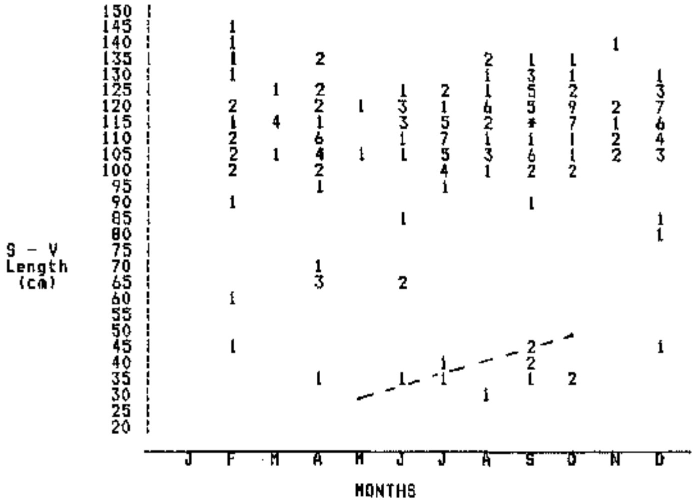


Figure 14 (b) Body size - month matrix showing the seasonal distribution in s-v length according to the month of collection for all female L. colubrina caught on the islands of S. E. Viti Levu. Sample size = 207. The inferred juvenile growth rate is shown as a broken line. (Numbers = individuals of a given s-v length class caught in a specific month. * indicates more than 10 specimens in the class for that month.)

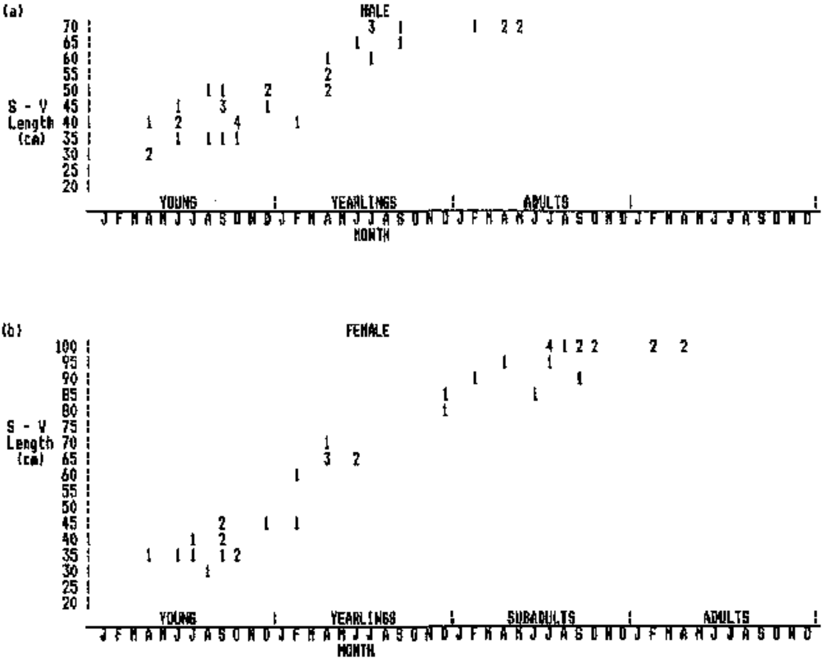


Figure 15. The inferred growth of male (a) and female (b) L. colubrina based on the month of capture. Numbers indicate the number of individuals caught in a size class in a month.

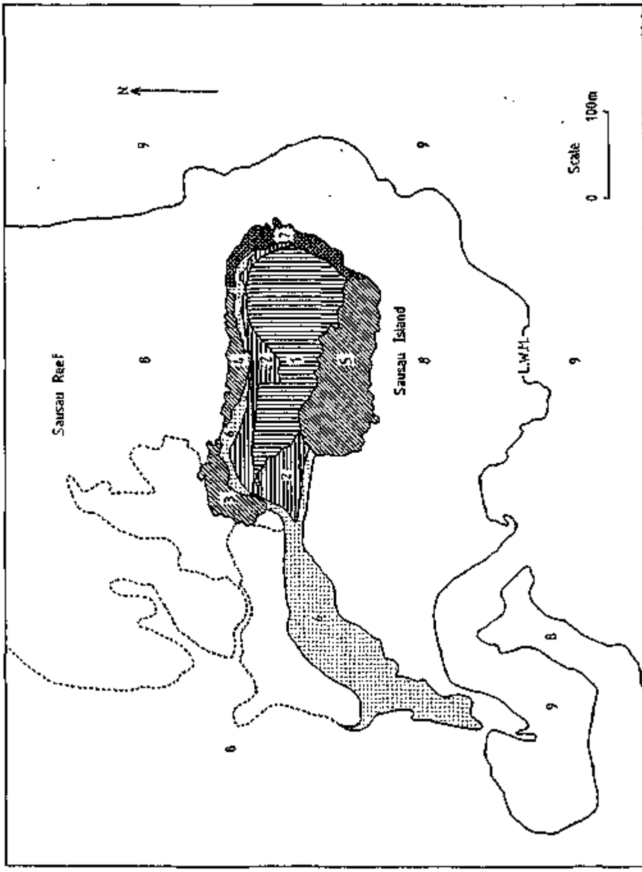
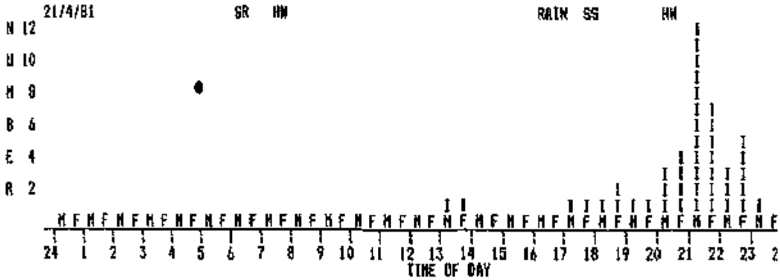


Figure 16. Sausau Island divided into habitats. (1) elevated centre o the island. (2) tall grass and coconut palms on sand. (3) mangroves. (4) mangroves. (5) mangroves. (6) sandspit. (7) rocky windward area. (8) reef flat. (9) open water. See text for further descriptions.


21/4/81
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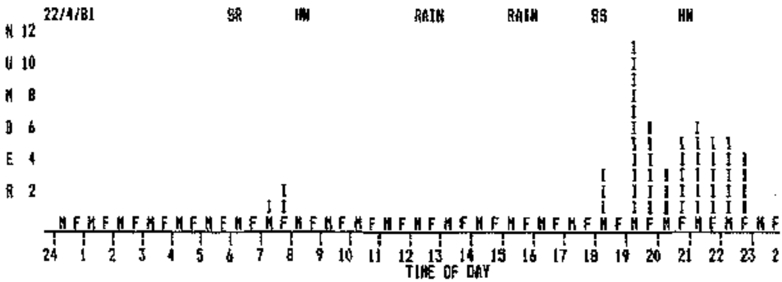
TIME OF DAY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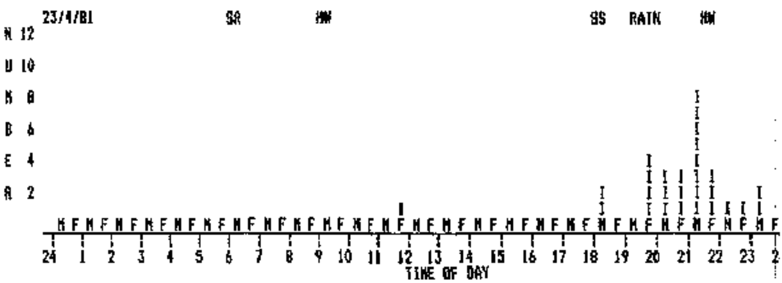
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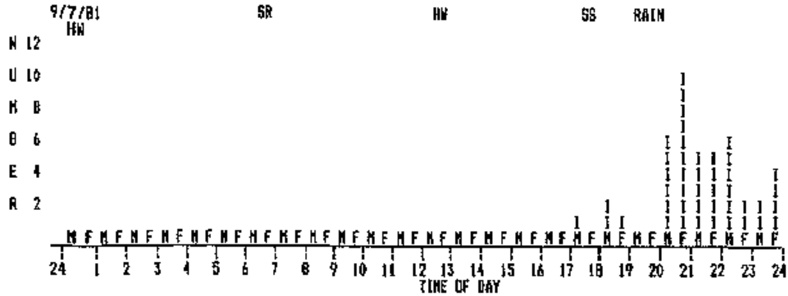
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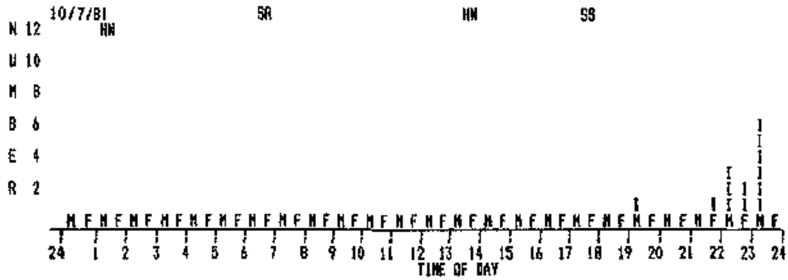
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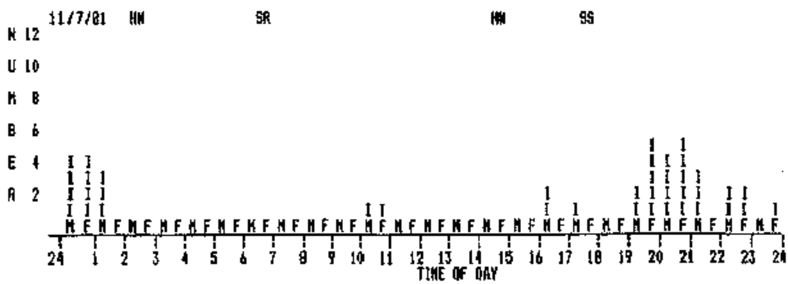
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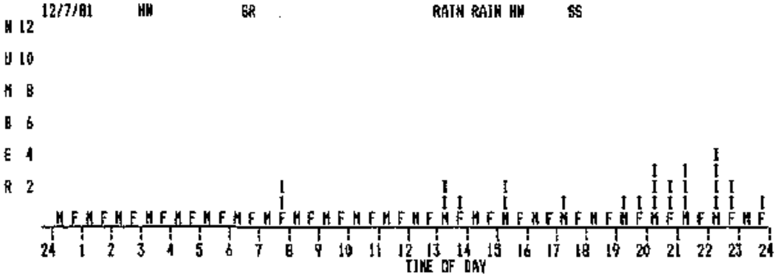
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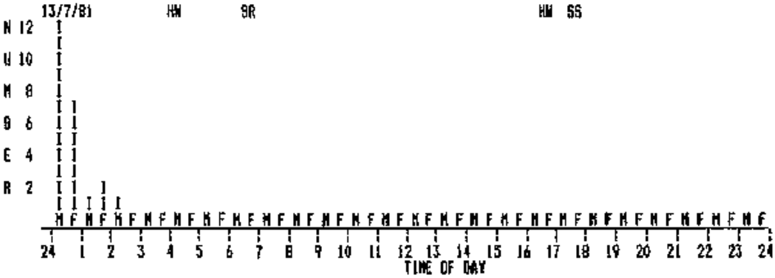
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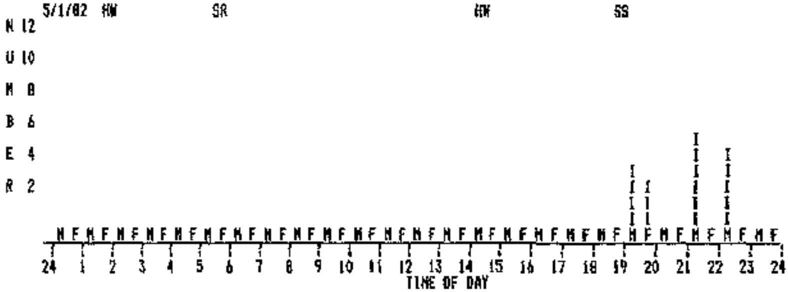
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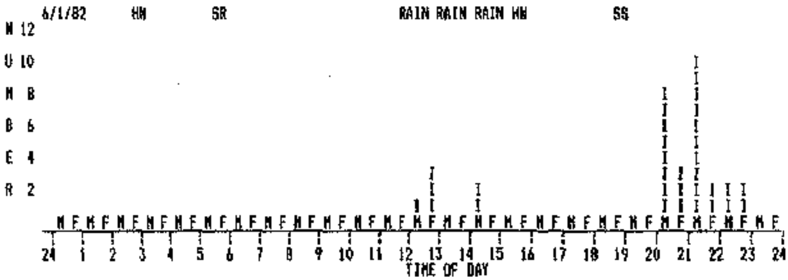
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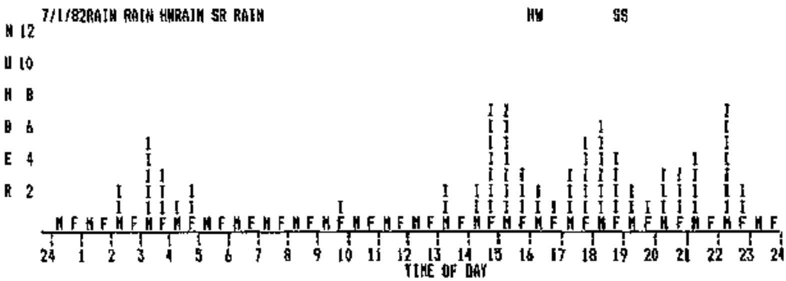
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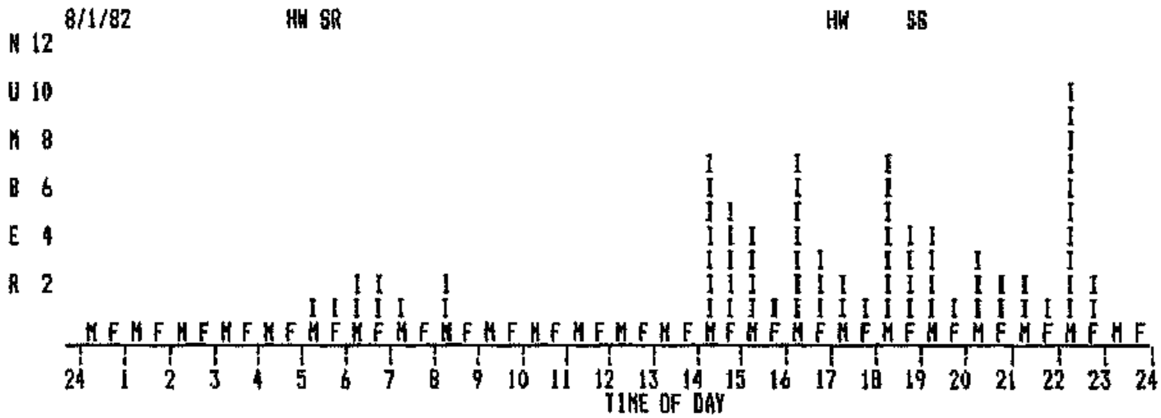
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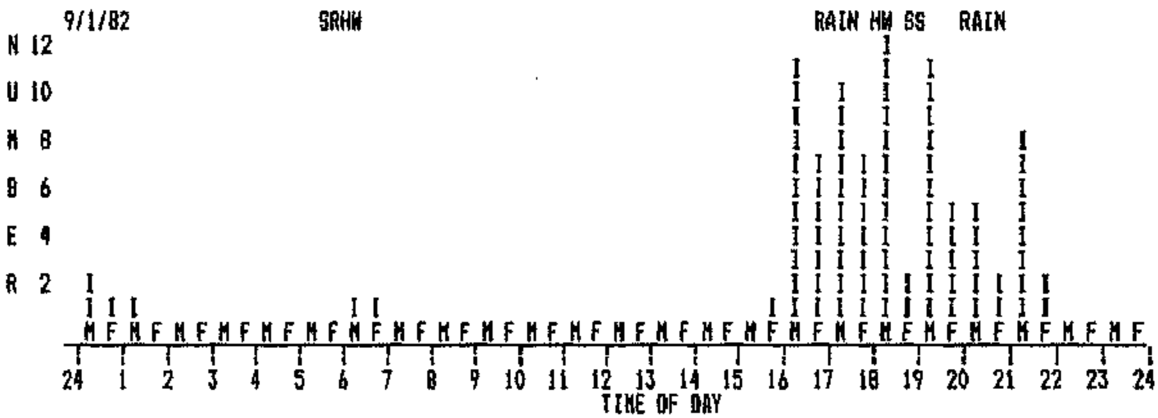
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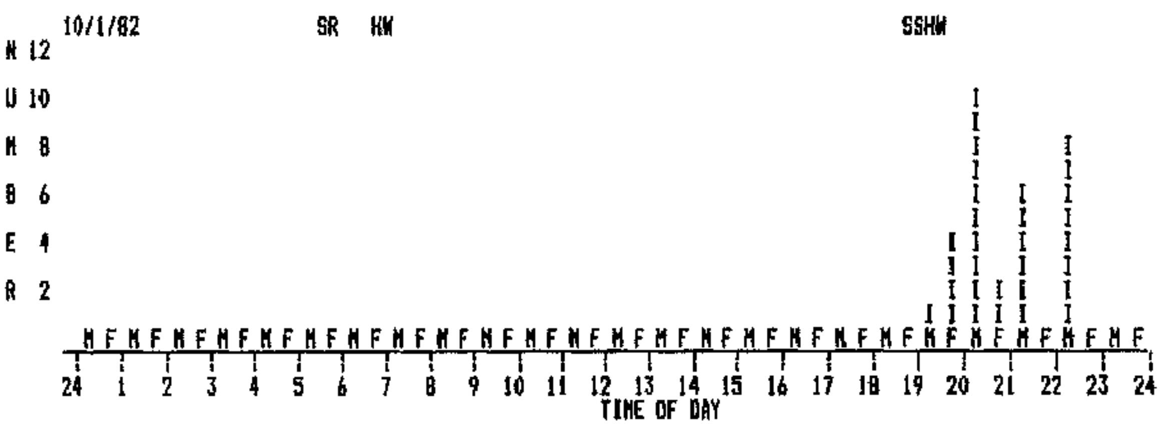
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SR
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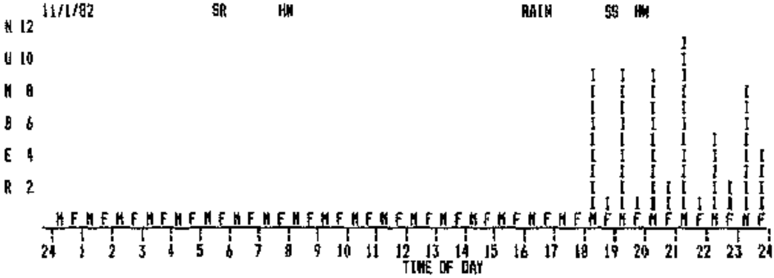
NUMBER
TIME OF DAY



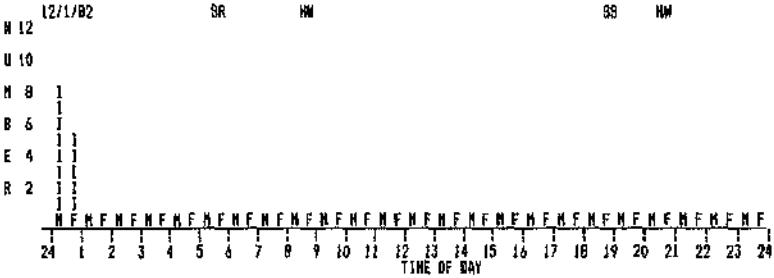
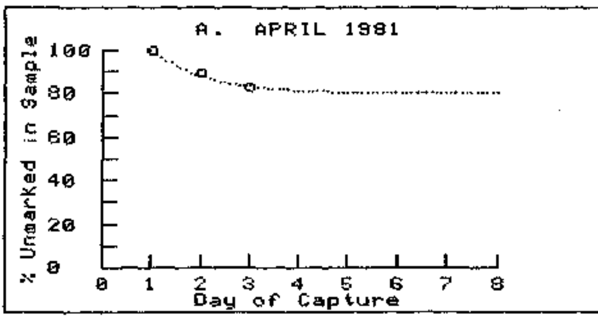
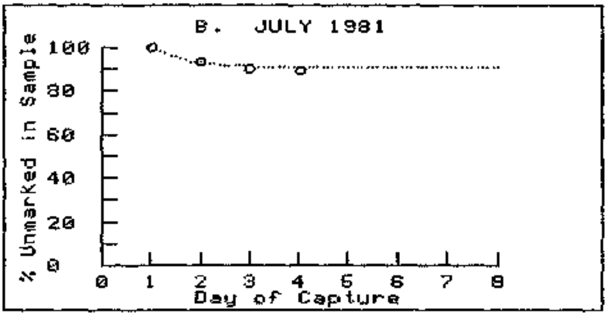
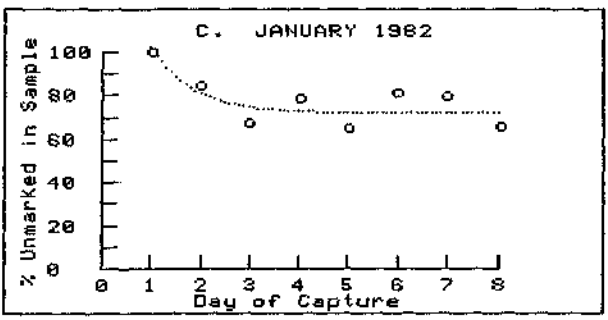


Figure 17. The figure shows the frequencies of active male and female L. colubrina for the twenty-four hours for each visit to Sausau Island. The date of each visit appears at the top of each figure. The approximate position of sunrise (SR) and sunset (SS), high water (HW) and periods of rain (Rain) are placed beside the date to coincide with the appropriate hourly intervals.

Figure 18. The daily recruitment (% unmarked per day) on Sausau Island for April (a), July (b) and January (c). The percentage unmarked in each twenty-four hour capture period have been fitted to the equation $y = a + b \times c^{x}$ (Limpus _et al._,1984). The asymptotic value for each month indicated the percentage of the land population that moved between the shore and the sea each day. Values were; April, 80 ± 1.7%; July, 91 ± 1.8%; January, 72 ± 10.2%.




B. JULY 1981
% Unmarked in Sample
100
80
60
40
20
0
0
1
2
3
4
5
6
7
8
Day of Capture


C. JANUARY 1982
% Unmarked in Sample
100
80
60
40
20
0
0
1
2
3
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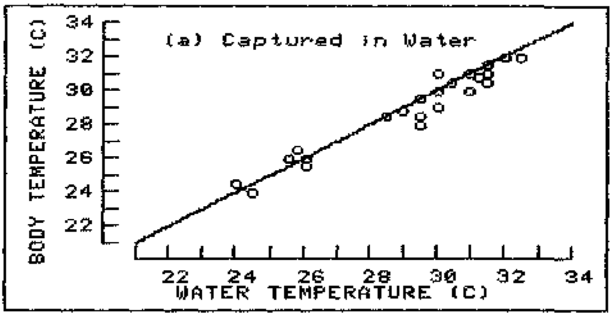
5
6
7
8
Day of Capture

Figure 19. Body temperature of L. colubrina and that of the immediate environment. The body temperature of L. colubrina in water (N = 31) was close to that of the surrounding water (a). The body temperature of snakes moving on land (N = 63) deviated from air temperature (b). Most specimens had body temperatures higher than the air temperature. The body temperatures of resting snakes (N = 67) were mostly higher than those of the ground (c). The body temperatures of resting snakes (N = 146) were mostly higher than those of the immediate air (d). The straight line of body temperature equals environmental temperature is shown in each graph. See text and Table 18 for further information.



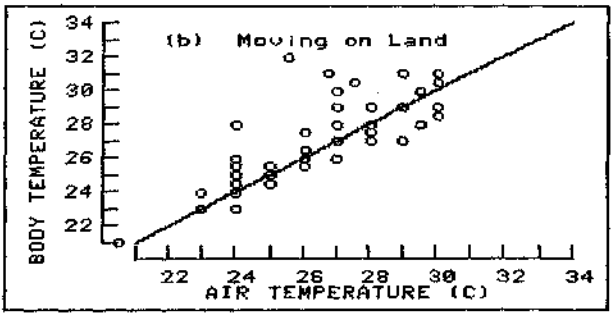
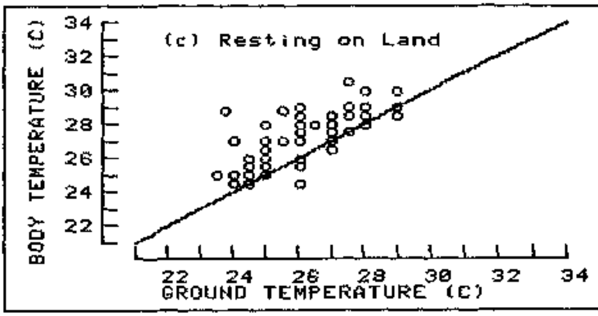


Figure 19(a) upper; Figure 19(b) lower



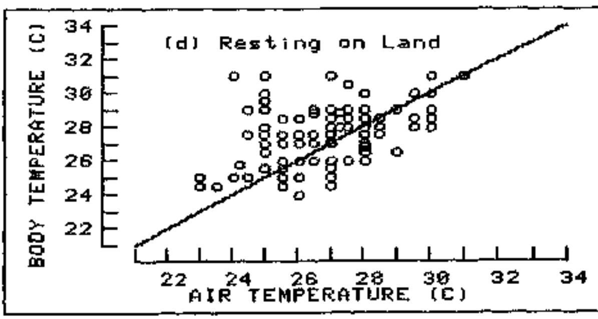


Figure 19(c) upper; Figure 19(d) lower

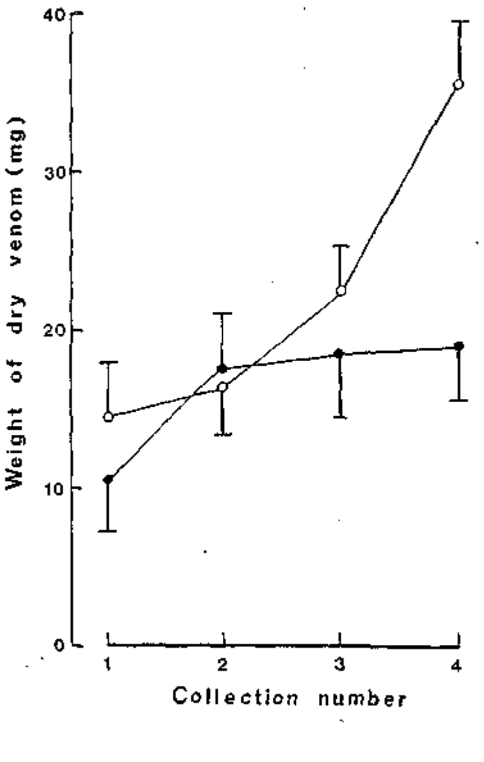


Figure 20. Effect of regular venom collection on dry venom yields. Venom was collected from Group I (solid circle, supplied with water) and Group II (open circle, water deprived) animals on four occasions at weekly intervals.

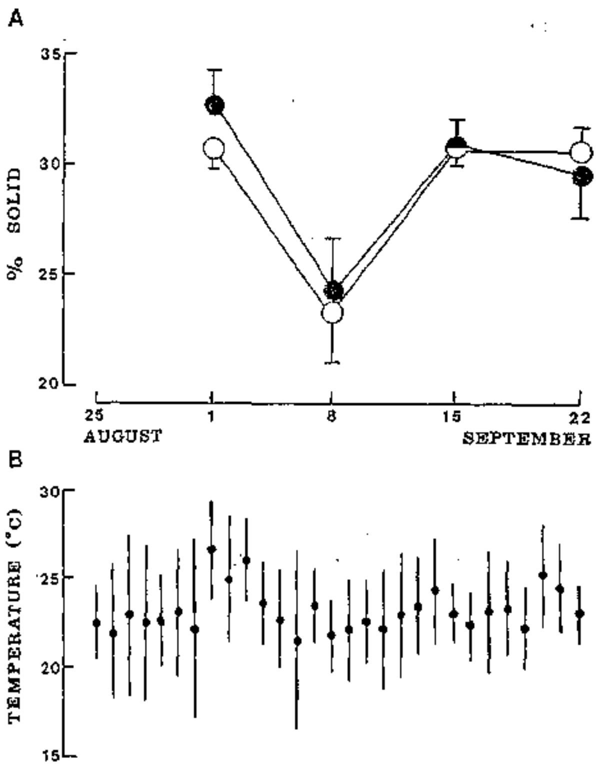


Figure 21. Effects of regular venom collection on the amount of solid in whole venom.

A: % solid in whole venom collected at weekly intervals. The snakes arrived in the laboratory on August 25 and were milked at weekly intervals i.e. September 1, 8, 15 and 22. Group I (solid circle) were supplied with water. Group II (open circle) were water deprived.

B: Daily temperature means and ranges (degrees Celsius) for the period of venom collection.

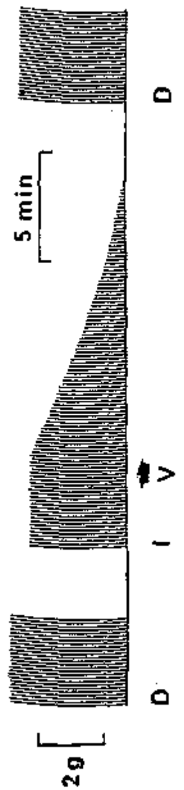


Figure 22. Effects of venom (4.9 μg/ml) on responses of the chick biventer cervicis nerve-muscle preparation to indirect (I) and direct (D) stimulation. The venom was added at the arrow.

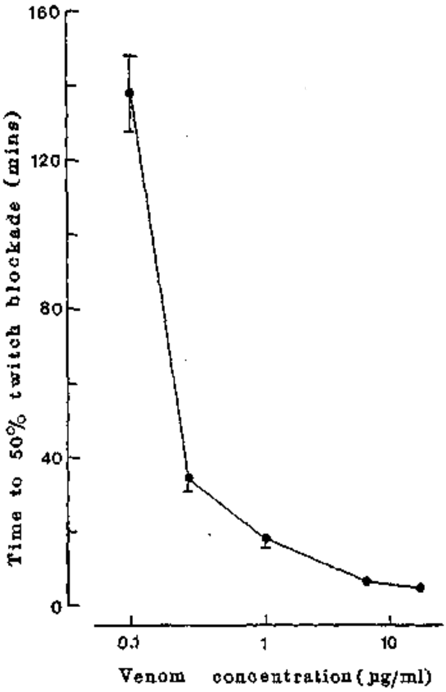


Figure 23. Neuromuscular blocking potency of dry venom on the chick biventer cervicis preparation. The time (in minutes) to reduce indirectly elicited contractions (in µg/ml). Each point represents the mean of 4-8 determinations and the bars indicate the standard error (unless smaller than the symbols).

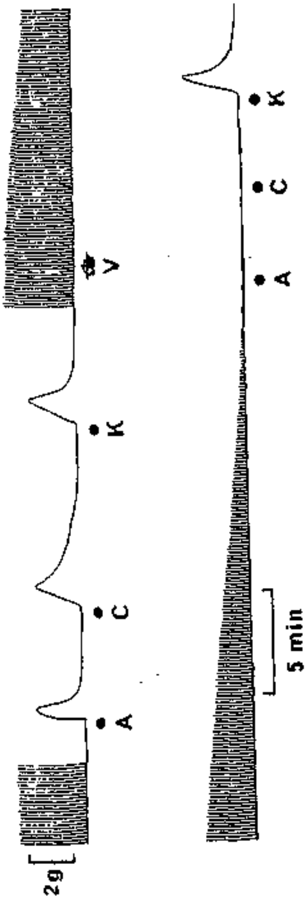


Figure 24. Action of dry venom (1.9 µg/ml) on the chick biventer cervicis preparation.

Top Panel: Control responses to indirect stimulation, acetylcholine (A, 3 X 10^{-4}M), carbachol (C, 2 X 10^-[illegible]M) and KCL (K, 3 X 10^{-2}M). Venom (V, 1.9 µg/ml) was added at arrow during indirect stimulation.

Bottom Panel: After complete blockade of responses to indirect stimulation there was no response to either acetylcholine or carbachol when added at the same concentration as before, but the KCl response was similar to control.

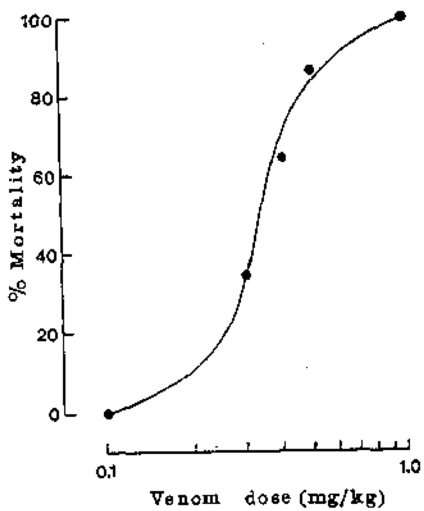


Figure 25. Log dose - mortality curve for lyophilised venom in mice.

PLATES

Plate 1 (a).

Plate I (b). The common Fijian sea snake Laticauda colubrina. The yellow colour of the upper lip is diagnostic of the species. A parasitic tick, Amblyomma nitidum (a) is attached to the head. The flattened paddle-like tail aids swimming (b).

Plate 2. Laticauda laticaudata although common in some areas of the South Pacific, was rare in present study in Fiji. This specimen (RA 142) was collected from Toberua Island in Bau Waters.

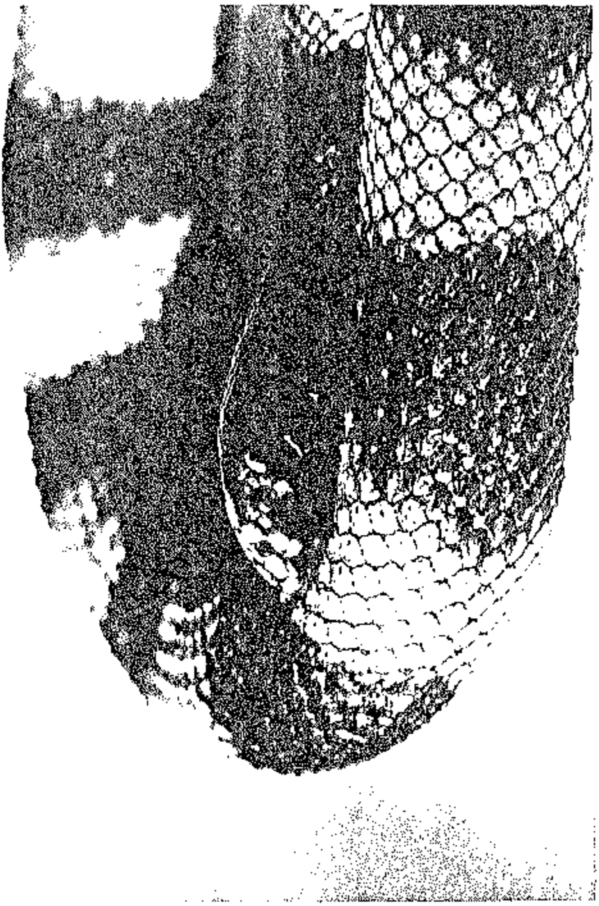


Plate 3. Hydrophis melanocephalus was relatively common in inshore lagoonal waters in Fiji.

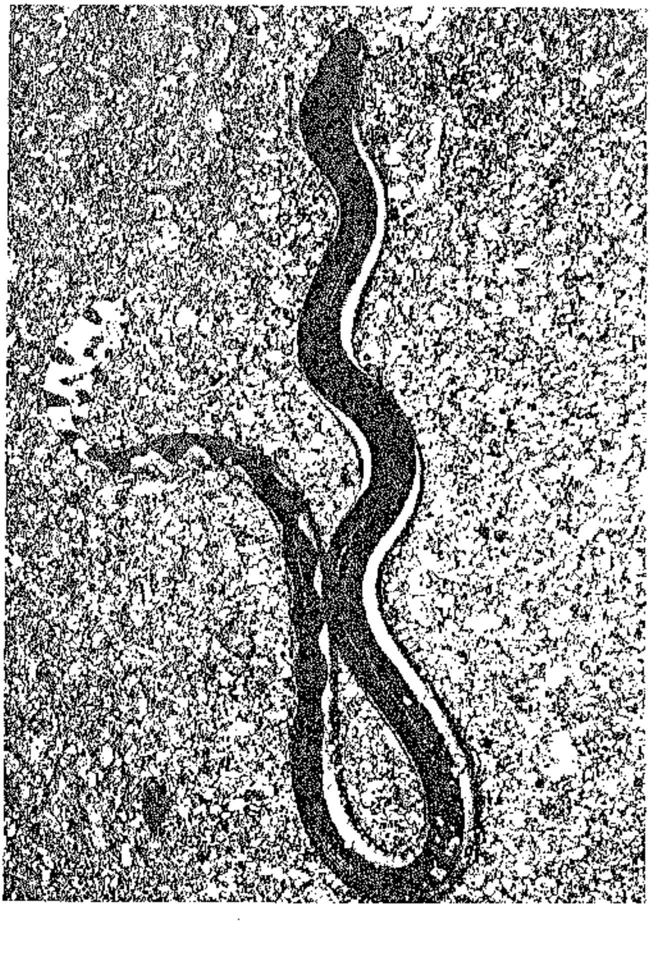


Plate 4. Pelamis platurus was caught in open water between islands. It rarely ventured into coastal waters. Photograph by Paddy Ryan.

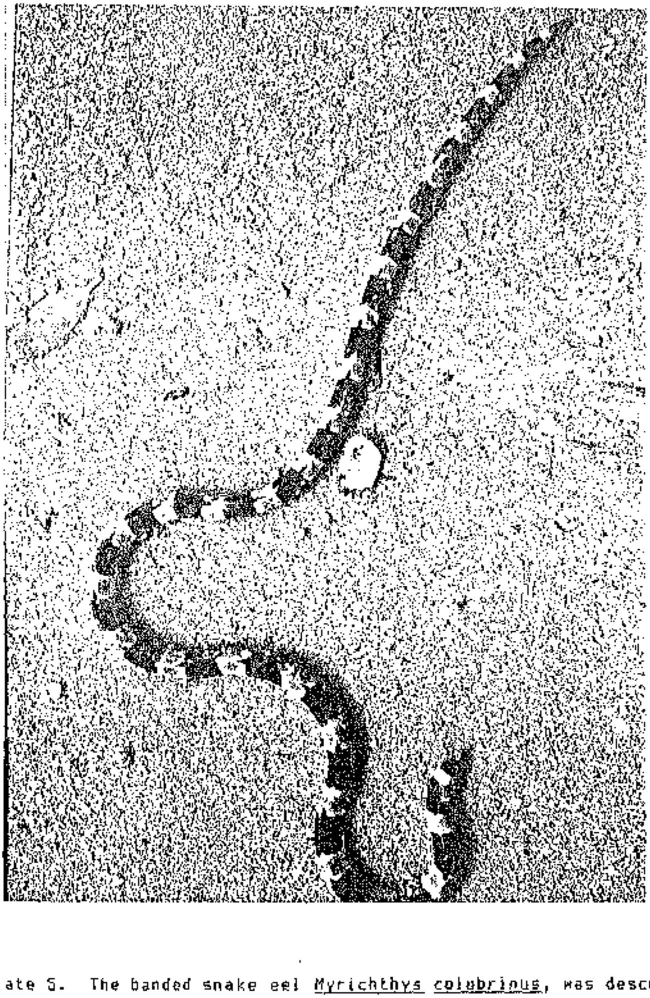


Plate 5. The banded snake eel _Myrichthys colubrinus_, was described as a mimic of _L. colubrina_ by Pernetta (1977). Snake eels were found in sandy areas throughout the study areas during the day.

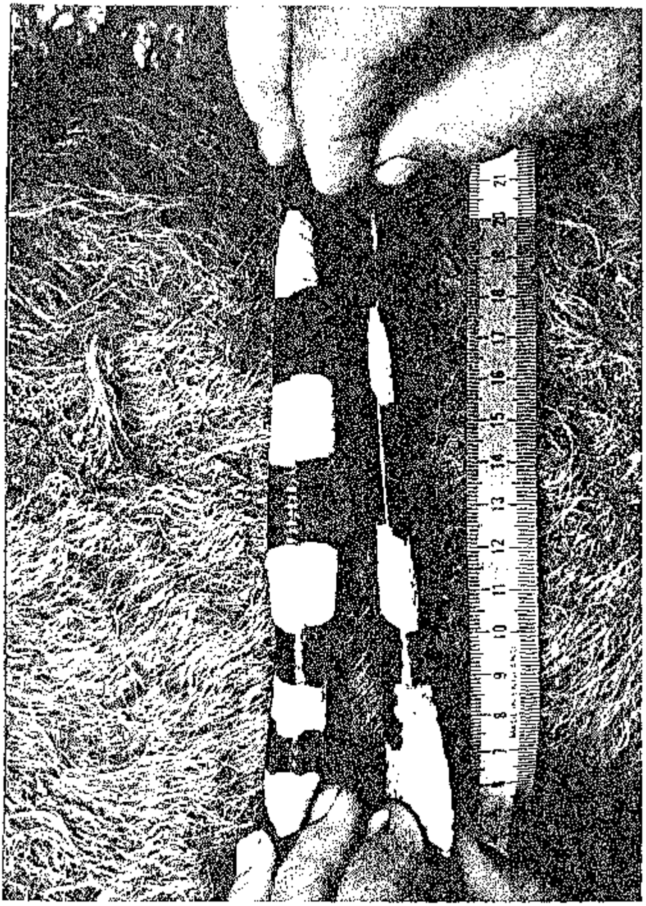


Plate 6. The shape and thickness of the tail was the most obvious difference between adult male and female L. colubrina. The tail of an adult male (top) is enlarged ventrally to accommodate the hemipenes. Female tails (bottom) lacked this enlargement.

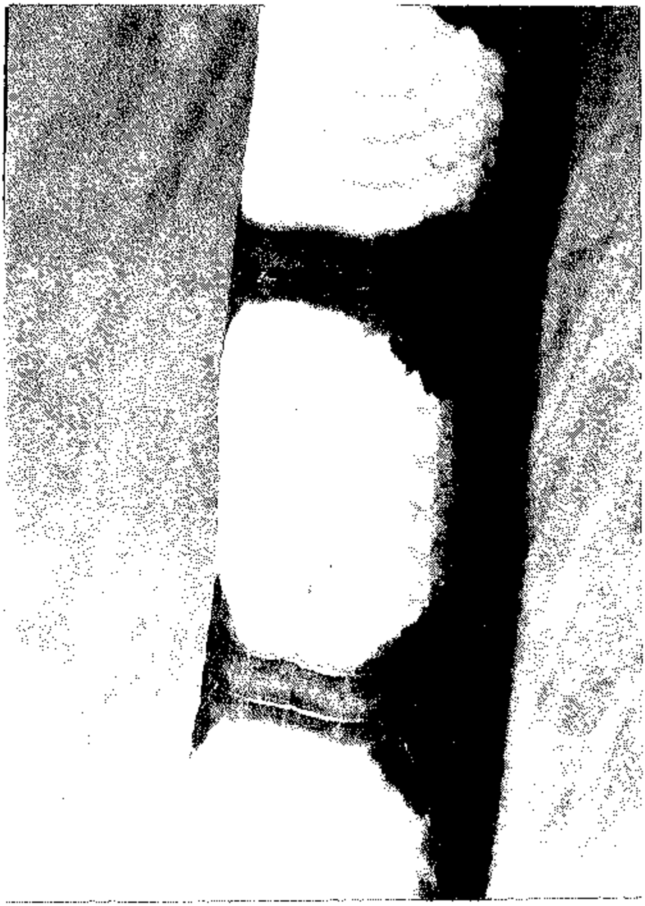


Plate 7. Aberration in ventral scales of L. colubrina was often in the form of half scales. A half scale on one side of the body was usually compensated for by a half scale further along the body.

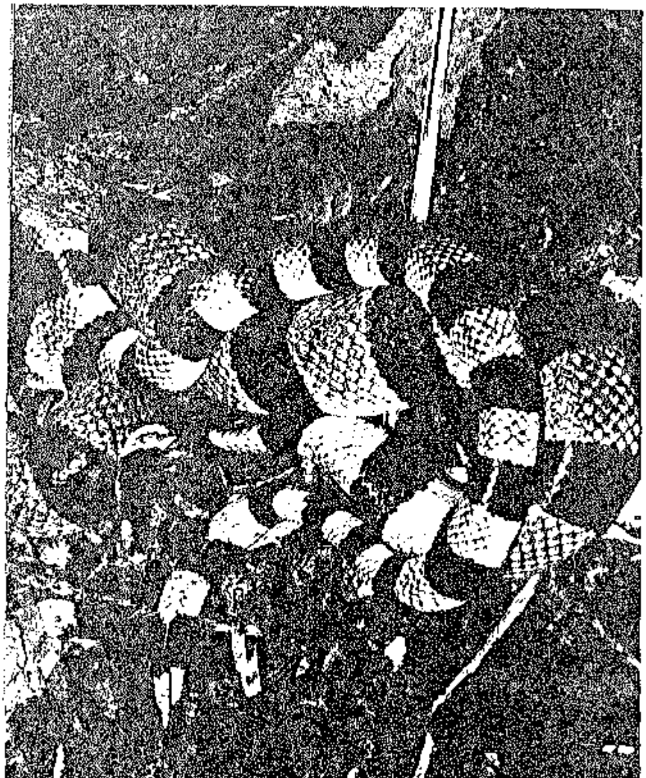


Plate 8. Copulation in L. colubrina took place on land. The male (smaller of the specimens) maintains close body contact with the female.

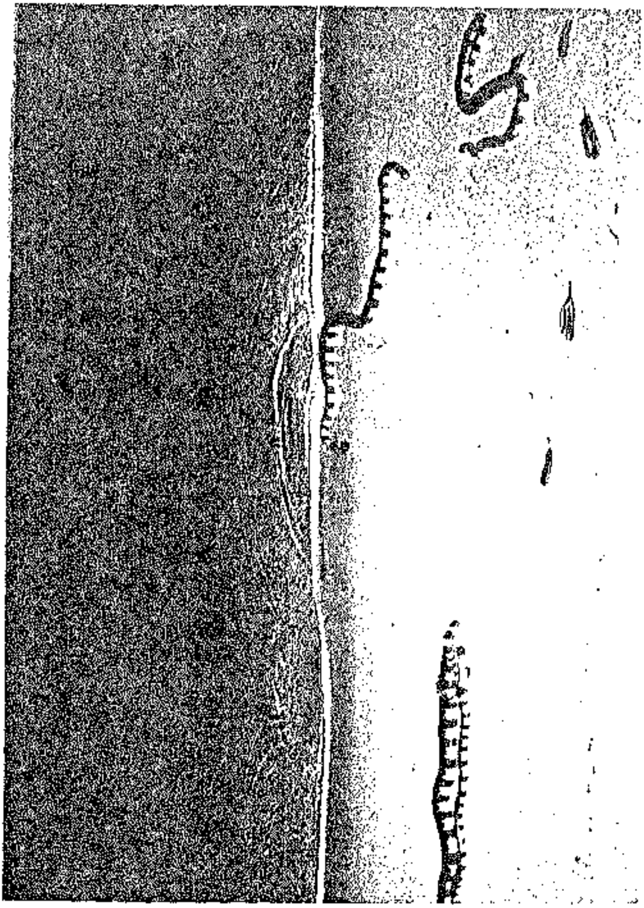


Plate 9. Males leave the water where a female has emerged. This position was located by males moving parallel to the water's edge and sensing the beach with their tongue.

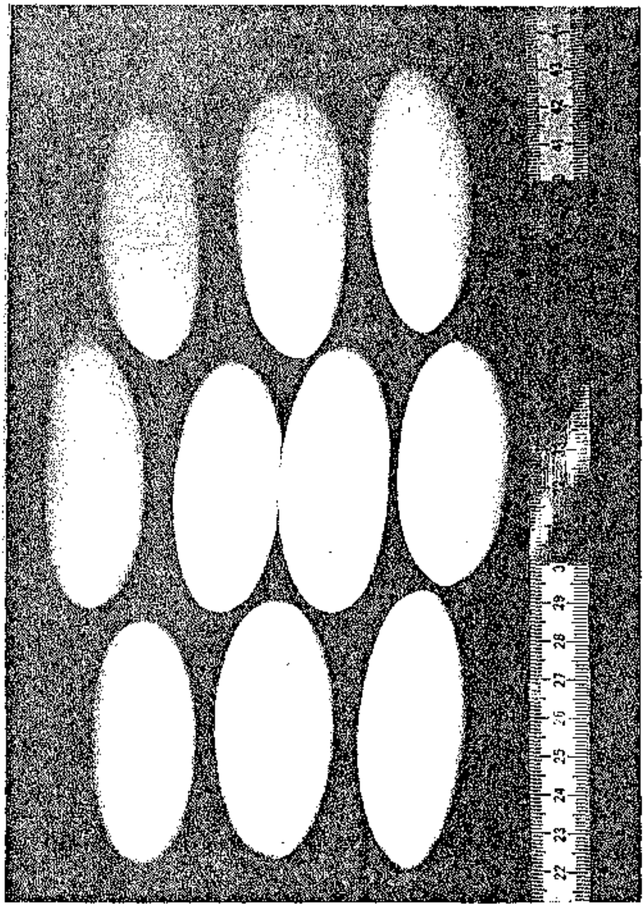


Plate 10. A clutch of eggs from a female L. colubrina held in captivity.

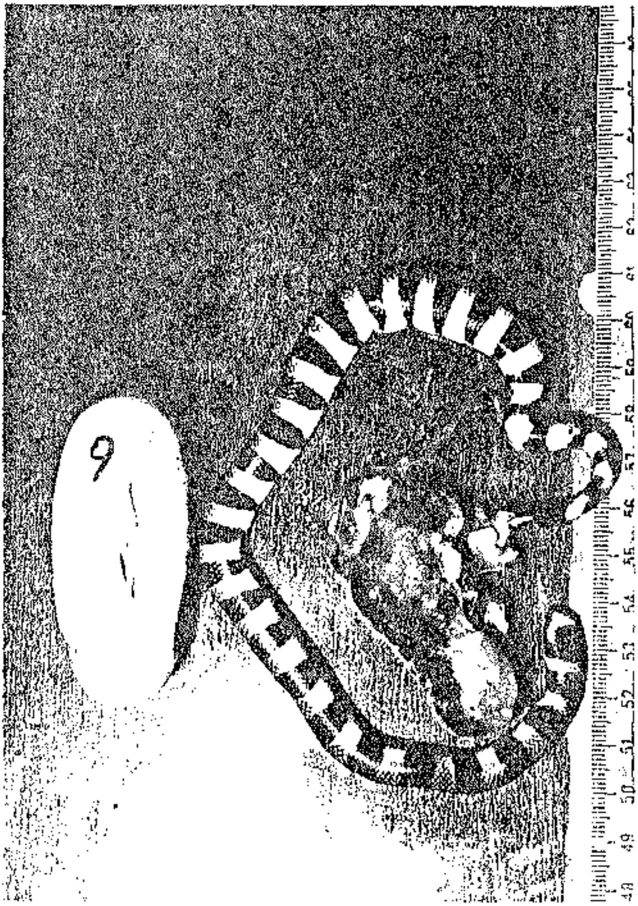


Plate 11. A newly hatched juvenile L. colubrina showing the eggshell and extra-embryonic membranes. See text for details.

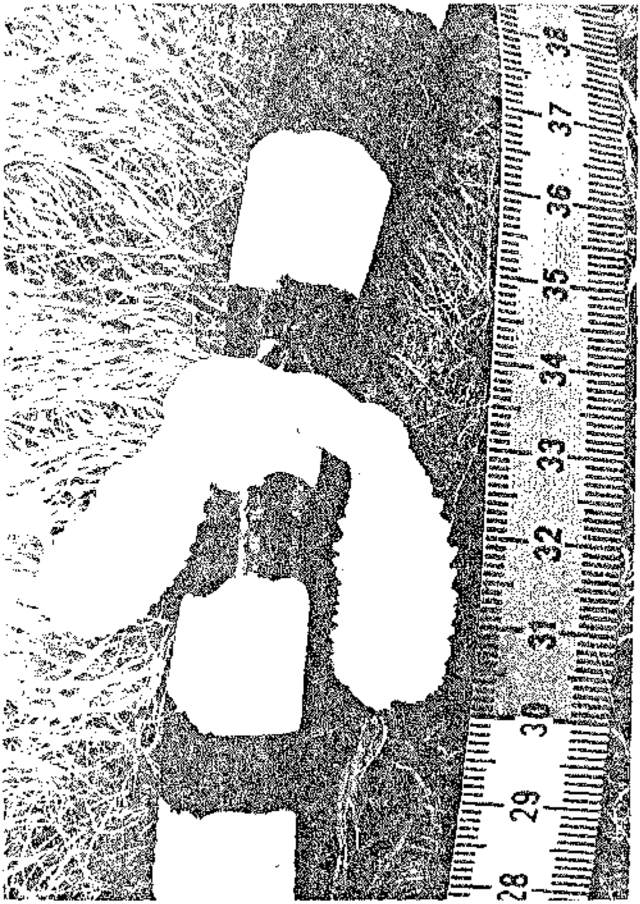


Plate 12. The paired hemipenes of a male L. colubrina. Each hemipenis was inflated with water to show the smooth proximal base, the region of large spines, the distal portion covered in calyces and the bifid tip. See text for details.

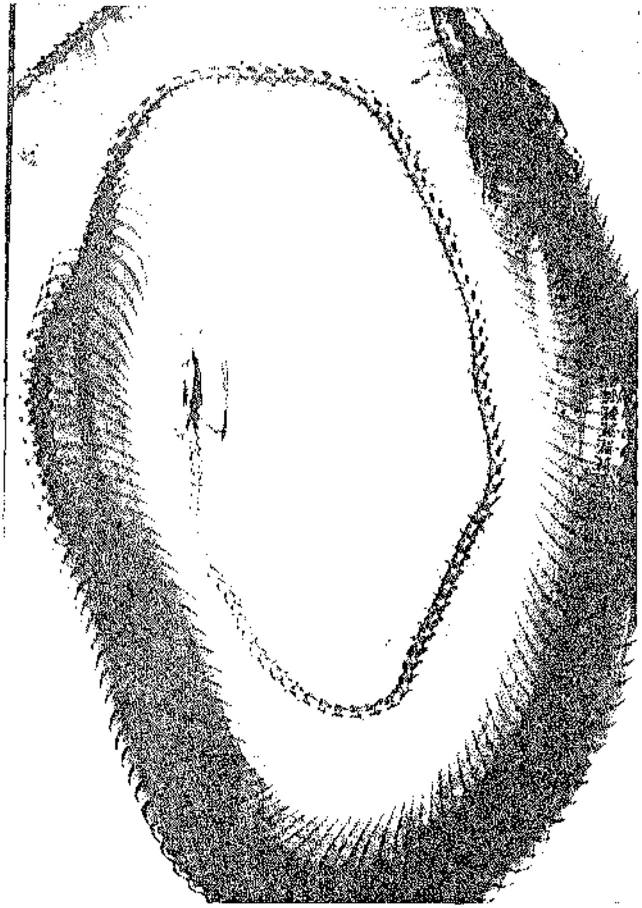


Plate 13. This radiograph of a female L. colubrina with its stomach contents of an eel (Gymnothorax sp.) shows the relative size of the eel to the snake. Only the head of the eel is positioned in the stomach, the remainder is in the oesophagus.

Plate 14. Juvenile L. colubrina are vulnerable to attack by intertidal crabs. The portunid crab (Thalamita crenata ?) photographed has captured a juvenile snake as it approached the shore. Although not killing the snake immediately, it has eaten the flesh to expose the backbone which would lead to the death of the prey.

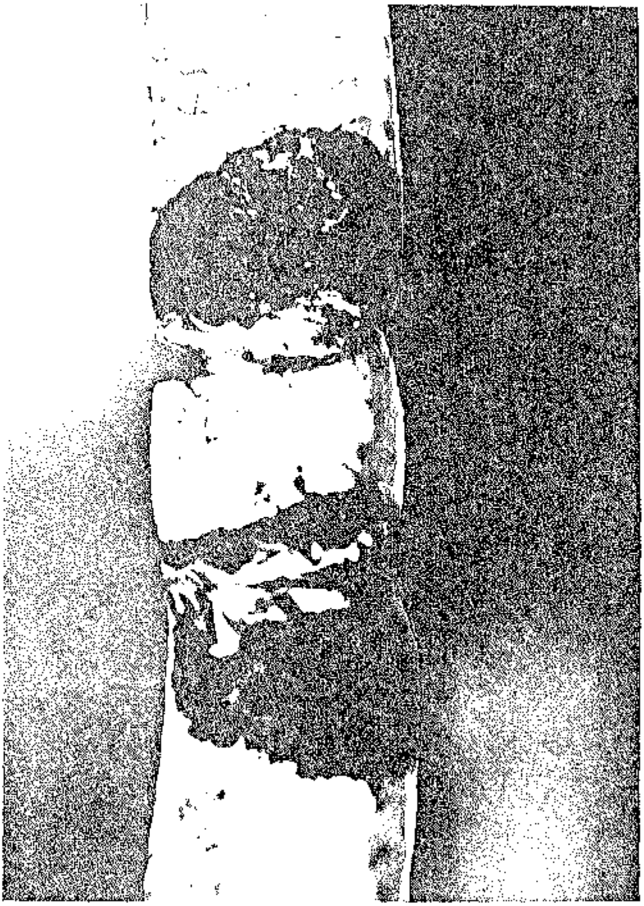


Plate 15. A commonly encountered scar on the bodies of adult L. colubrina is shown by this photograph. Two parallel wounds about 2 cm apart encircle the body. The origin of such scars is not known, but is assumed to be caused by a crab.

Plate 16. Adult L. colubrina that inhabited grassy areas on Sausau Island were vulnerable to grass fires. Individuals showed no fear of fire and many were killed while resting.

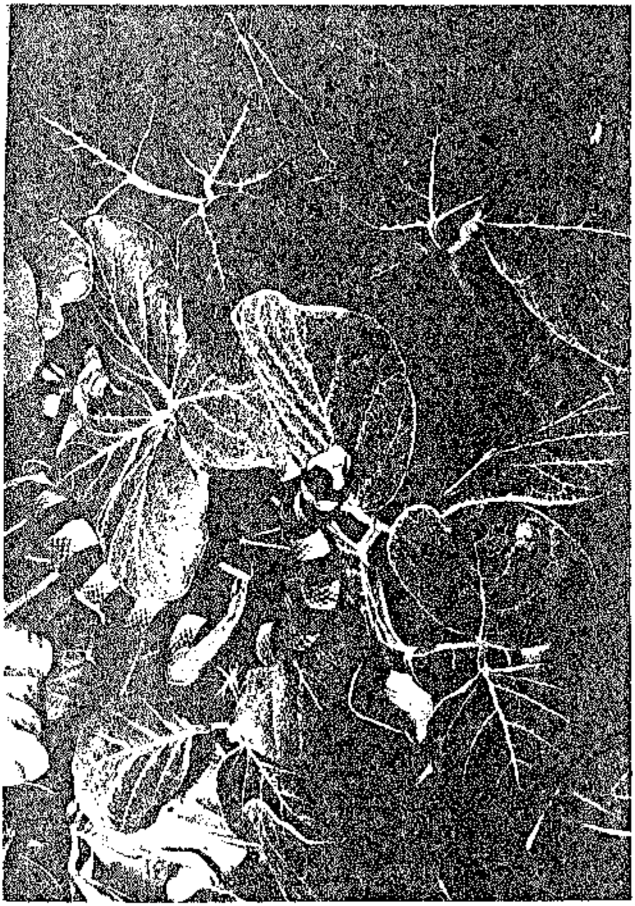


Plate 17. During periods of drought on Sausau Island, L. colubrina were active at night drinking water droplets that had collected by guttation on the leaves of vegetation.

Plate 18. The venom gland and venom duct are outlined by the injection of indian ink into the gland before it cleared and stained. The venom duct is a single structure on each side of the head in the supralabial position. There is no branching of the venom duct as suggested by Halstead (1978).

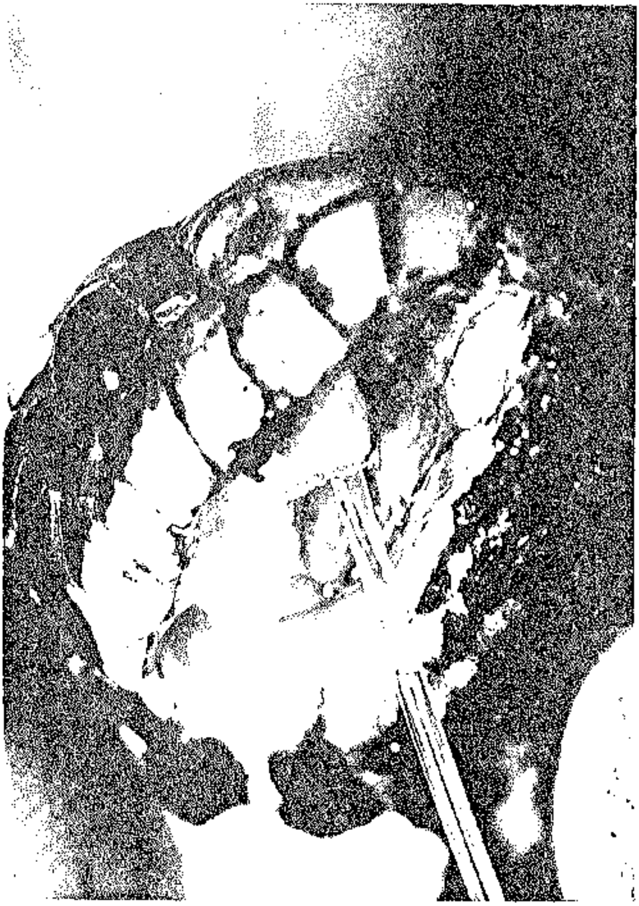


Plate 19. Venom was collected by dislocating the jaws and placing a length of clean plastic tubing over each fang in turn. Venom was released when the tubing touched the mucous membranes.

APPENDIX

A. This programme is a BASIC version of that published by Caughley (1977) to estimate the size of a population from the recapture frequency.

```
 40  LET D$ =  CHR$ (4)
 50  DEF  FN G(X) =  EXP ((X - .5) *  LOG (X) - X + .918 +
     (1 / (12 * X)) - (1 / (360 * X ^ 3)))
 90 S1 = 0:S2 = 0:S3 = 0
 95  PRINT " HOW MANY TIMES WERE THE ANIMALS SAMPLED? ": INPUT "";N
 100  DIM F(N),E(N)
 105  PRINT " # OF ANIMALS CAPTURED "
 110  FOR I = 1 TO N
 120  PRINT I;" TIMES = ";: INPUT "";F(I)
 130 S1 = S1 + F(I)
 140 S2 = S2 + F(I) * I
 150 S3 = S3 + F(I) * I ^ 2
 160  NEXT I
 170 A = S2 / S1
 180 VA = (S3 - (S2 ^ 2) / S1) / (S1 - 1)
 190 M = A - VA * F(1) / (A * (S1 - F(1)))
 200 FO = (S2 - M * S1) / M
 210 N1 = S2 / M
 213  PRINT "PRESS P FOR A PRINTOUT "
 214  PRINT "PRESS ANY KEY TO CONTINUE"
 215  GET P$: PRINT : IF P$ = "P" THEN  PRINT D$;"PR#1"
 230  PRINT " NEGATIVE BINOMIAL "
 250 W = A / VA * (1 - F(1) / S1)
 260 K = (W * A - F(1) / S1) / (1 - W)
 270 H = 1
 280  FOR I = 1 TO N
 290 H = H * I
 300 E(I) = S1 * (W ^ K) / (1 - W) *  FN G(K + I) /
     ( FN G(K) * H) * (1 - W) ^ I
 310  NEXT I
 320  GOSUB 1000
 325  PRINT : PRINT
 370  PRINT " F ZERO = ";FO
 380  PRINT " POPULATION ESTIMATE = ";N1
 390  PRINT " CHI SQUARE = ";X2
```

```
400  PRINT " DEGREES OF FREEDOM = ";N - 3
405  PRINT : PRINT
410  PRINT " GEOMETRIC ESTIMATE "
420 Q = (S2 - S1) / (S2 - 1)
425  FOR I = 1 TO N
430 E(I) = S1 * (1 - Q) * Q ^ (I - 1)
440  NEXT I
445 N2 = S1 / Q
450  GOSUB 1000
480  PRINT " POPULATION = ";N2
490  PRINT " CHI SQUARE = ";X2
500  PRINT " DEGREES OF FREEDOM = ";N - 2
505  PRINT : PRINT
510  PRINT " POISSON ESTIMATE "
520 TM = A
530 TM = TM - .001
540 ES = TM / (1 -  EXP ( - TM))
550 T = A - ES
560  IF T < 0 GOTO 530
570 N3 = S2 / TM
575 TT = S2 / TM
580  PRINT " POPULATION = ";N3
590  PRINT " T MEAN = ";TM
600 DI = TT *  EXP ( - TM)
610  FOR I = 1 TO N
620 DI = DI * TM / I
625 E(I) = DI
630  NEXT I
640  GOSUB 1000
680  PRINT " CHI SQUARE = ";X2
690  PRINT " DEGREES OF FREEDOM = ";N - 2
695  PRINT D$;"PR#0"
700  END
1000 X2 = 0:X1 = 0
1005  PRINT "#  OBS   EXPECTED   CHI SQ"
1010  FOR I = 1 TO N
1020 X1 = ((F(I) - E(I)) ^ 2) / E(I)
1025  PRINT I;"   ";F(I);"   ";E(I);"   ";X1
```

```
1030 X2 = X2 + X1
1040  NEXT I
1050  RETURN
```

=====