

ECOLOGY AND FEEDING BEHAVIOUR OF THE
TASMANIAN TIGER SNAKE
NOTECHIS ATER HUMPHREYSI

by

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FIG. 1 *NOTECHIS ATER HUMPHREYSI*, EXHIBITING OFFENSIVE THREAT.



GENERAL INTRODUCTION

Although the ecological and behavioural aspects of the biology of reptiles have received increased attention in the last two decades, in general, research activities have been centered around families containing representatives that are relatively innocuous and/or of small individual size, particularly those of the North American continent and some areas of Europe. The ecology and behaviour of small lizards has been studied by several investigators, including Carpenter (1960), Sexton and Heatwole (1968), Ballinger, Marion and Sexton (1970), Ballinger and Schrank (1970), Kour and Hutchinson (1970), Avery (1971) and Fitch (1972). Lizards of the family Iguanidae have been investigated in considerable detail and the voluminous literature relating to this taxon includes studies by, Carpenter (1961), McGinnes and Dickson (1967), Halpern and Lowe (1968) and, White (1973).

A substantial amount of information is also available about crocodilians and chelonions, as well as about colubrid snakes, e.g. Shaw (1951), Carpenter (1952), Dmi'el (1967), Burghardt (1969), Gillingham (1974) and Greenwald (1974).

Although Australia is distinguished by possessing an abundant and diverse herpeto-fauna (664 species distributed over some 21 families) research on the reptiles of this has been negligible until the early-to mid-1960's. During the latter period, detailed investigations have focused on the geckionids, Bustard (1965, 1968b and 1969a), the skinks, Bently (1959), Bartholomew *et al.* (1965), Barwick *et al.* (1966), Dawson *et al.* (1966) and Hamel *et al.* (1967) and the agamids, Bently and Blumer (1962), Licht *et al.* (1966a and 1966b), Bradshaw and Main (1968) and Pianka (1971a), and these studies have produced impressive quantities of data. However, until the last decade, research on the larger venomous snakes has been principally confined to some of the crotaline species of North

America (e.g. Fitch 1949, Whaton 1966 and Kardong 1975), and European viperids (e.g. Prestt 1971). Studies on Australian representatives have been restricted to a series of investigations by Spellerberg (1972) on the thermoregulatory activities of some species of elapid snakes, and investigations by Shine (1977, 1979 and 1980).

Sixty five of the total number (110) of the terrestrial snakes thus far recorded in Australia, belong to the family Elapidae. The majority of Australian elapids are only slightly venomous and are, therefore, not considered to be a serious hazard to man. Known species range in size from twenty cm (*Brachysophis wood-jonesi*), to 3 m (*Oxyuranus scutalatus*). The majority of the larger, more venomous, species are relatively common along the eastern and southern coastal areas of Australia. The tiger snake (*Notechis s. scutatus*), the red-bellied black snake (*Pseudochis porphyriacus*), the brown snake (*Pseudonaja textilis*) and the copper head (*Australaps superbus*), occur throughout rural, grazing areas as well as in virgin forests, in the eastern and southern states of the country (Cogger 1979).

The ecology of six species of Australian elapid snakes, including *N.s. scutatus*, *P. porphyriacus*, *P. textilis* and *A. superbus*, has been recently studied by Shine (1977), in the New England area of North-Eastern New South Wales. This study represents the first comprehensive investigation, conducted in natural situations, of the utilization of various habitats, food-resources, diet and considerations of sympatry in the larger Australian elapid snakes.

The present study is aimed at examining selected aspects of the ecology and feeding behaviour of a single elapid species of the genus *Notechis*; considered to be of particular interest in view of its extreme southerly distribution and occurrence in relatively cold climatic conditions. It is proposed to compare some of the characteristics of this species with those of venomous snakes occurring in the Northern Hemisphere as well as with those of elapid species of continental Australia, in terms of thermal ecology, activity-patterns, utilization of prey-species and feeding techniques.

MORPHOLOGICAL FEATURES OF THE SUBJECT:

A GENERAL DESCRIPTION

The subjects of the present investigation were specimens of Tasmanian tiger snakes, *Notechis ater humphreysi*, a melanic phase or sub-species of the genus *Notechis* occurring in various areas of the Australian continent. A typical individual of the Tasmanian form is illustrated in Fig.1. The precise taxonomic status (and affinities to the continental representatives of the tiger snakes) of *N.a. humphreysi* is a conjectural and contentious subject. For the purpose of this study, the classification and nomenclature proposed by Gow (1976) have been adopted because they are considered to be useful until the relevant problems are definitively resolved. According to this scheme, *N.a. humphreysi* is a sub-species of the nominate species which is represented on the mainland by the Peninsular tiger snake (*N.a. niger*), Krefft's tiger snake (*N.a. ater*) and the Chappell Island tiger snake (*N.a. serventyi*).

Individuals of *N.a. humphreysi* may attain total body lengths exceeding 1.5 m. The basic colour varies from greyish-brown (often patterned with yellow-fawn stripes) to completely black and unmarked by any pattern on the dorsal surface. The colour of the ventral surface varies from pale grey to yellowish. The head is generally broad and distinctly demarcated from the neck. The scales of the mid-body are arranged in 15 to 17 rows; the ventral scales number 161 to 174, the subcaudal scales 48 to 53 and the anal scale is single. As in all large elapids, the venom-apparatus is well developed and the effects of the venom are mainly neurotoxic although a haemorrhagic component is also present.

DISTRIBUTION OF *N.A. HUMPHREYSI*

The island state of Tasmania comprising an area of approximately 80,000 km², lies ca. 300 km to the south of continental Australia at 42°00S - 147°00E. The Tasmanian tiger snake occurs on King Island and surrounding islands of the Bass Strait, as well as on the main landmass of the state. The last land bridge to connect Tasmania to the mainland was submerged under the rising waters of Bass Strait some 12,000 years ago. Consequently, the Tasmanian species of *Notechis* has been isolated from other species of the genus for at least this period of time.

Documentation of the general habits, ecology or detailed behaviour of this species has been scant, although Cogger (1979) suggested that it is distributed over a wide range of habitats, ranging from dry, rocky areas to marshland and coastal dune-grassland. The species is viviparous, its diet is largely composed of frogs and small mammals (Cogger 1979). Worrell (1963) has recorded incidents of cannibalism in the King Island population of tiger snakes, and also stated that many of the coastal and island populations subsist, at least seasonally on the chicks of mutton birds, taken while they are in their nesting-burrows. Gow (1976) found that captive animals fed quite readily on day-old domestic chicks, mice and rats.

Within Tasmania, *N.a. humphreysi* is distributed throughout a considerable variety of habitat types from coastal heath at sea level, to highland forests above 1,000 m. Some habitats not inhabited by tiger snakes in Tasmania, are characterised by closed canopies with wet and/or dark substrates, (temperate rainforests) or alpine moorlands, occurring at high altitudes, possessing sparse, low-lying vegetation and occurring above the winter snow-line. Tiger snakes have adapted with conspicuous success to grazing-pastures, being common around farm dams and out-buildings in most areas of rural Tasmania. The occurrence of rainforests and alpine moorland is shown in Fig.2.

FIG.2 THE DISTRIBUTION OF RAIN-FOREST AND ALPINE VEGETATION-TYPES IN TASMANIA.



- Alpine Moorland

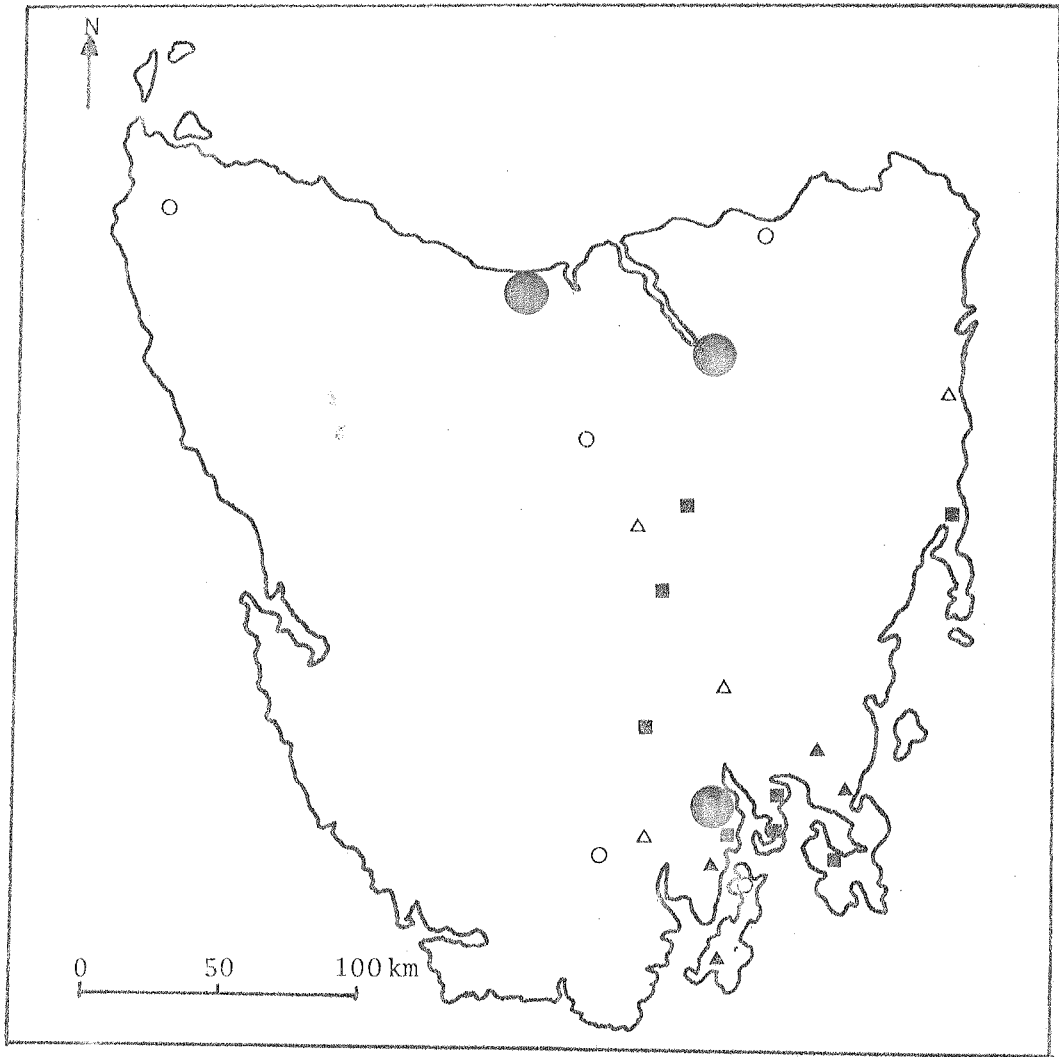


- Temperate Rainforests

Insert indicates the Lake Sorell area.

During a four year period from January 1977 to December 1980, the author has recorded 21 sites where specimens of *N.a. humphreysi* have been located. The distribution of these, illustrated in Fig.3, shows that the majority of sites of occurrence are situated in the south-eastern sector and range from coastal habitats to inland high-land habitats. Since precipitation is derived predominantly from western polar fronts, the eastern areas of Tasmania are generally drier than the areas of the western rainforest belts (Jackson 1972). The known distribution of *N.a. humphreysi* is, therefore, predominantly in regions of relatively low rainfall, although occasional records of the species inhabiting some of the more open habitats of the south-western sector are also available.

FIG.3 THE DISTRIBUTION OF *N.A. HUMPHREYSI* IN RELATION TO VARIOUS HABITAT-TYPES IN TASMANIA.
Data based on records of the author.



- △ - Rock outcrops
- ▲ - Fallen timber
- - Open grassland
- - Small rock outcrops in grassland
- - Population centres

CHAPTER 1

ECOLOGY

1.1 INTRODUCTION

Naturalistic, *in-vitro* observational studies of the life histories and/or habits of reptiles, unlike those of most avian or mammalian species, are often profoundly affected or even confounded by a single major complex of behavioural and physiological phenomena. These are usually described by the general term "hibernation" or torpor, denoting a state experienced by most species of reptile, particularly those occurring in colder climates, whereas birds and mammals usually remain active throughout the year. Consequently field investigations conducted in this study, similarly to many others, was limited to three months during which period the subjects were naturally active. Records of data were compiled in natural conditions only in this active period, before low temperatures induced torpor and the snakes finally retreated into the hibernacula.

Most poikilothermic animals are required to maintain, by active means, suitable body-temperatures to permit foraging activities and reproductive functions to be successfully performed. Studies on the thermoregulatory activities of several species of lizards (e.g. Heath 1964, Brattstrom 1971, and Garrick 1974), have clearly demonstrated that heliotherms maintain optimal body temperatures by behavioural mechanisms. Detailed investigations, discussed by Spellerberg (1972), Heatwole (1976) and Lillywhite (1980), suggest that the large Australian thigmothermic elapids also possess behavioural adaptations to thermoregulation in controlled laboratory conditions. Lillywhite (1980) has noted that although very little information is available about the body temperatures of elapid snakes under natural conditions, data obtained in the field by Heatwole (1976) correspond reasonably

well with the range and preferenda of body temperatures determined in laboratory studies.

The general feeding ecology and activity patterns of the larger elapid species of Australia are poorly documented, with the exception of a single series of investigations by Shine (1977 and 1979). These studies have established several facts, particularly that the large elapids of continental Australia are predominantly diurnal, occasionally exhibiting crepuscula activity and have relatively high preferred body-temperatures. Day-to-day movements were extensive, except in gravid females and the snakes were noted to over-winter singly, in shallow hibernacula.

The major objectives of the present study are to examine, under field conditions, the limiting factors affecting the distribution and daily activity-patterns of *N.a. humphreysi*. Since this species is a thigmothermic elapid experiencing relatively cold climates, its thermal ecology and thermoregulatory behaviour during basking and active periods were deemed to merit particular attention. Habitat utilization by the snakes was assessed within the study area in terms of the occurrence of individuals throughout several distinctive types of habitat. Foraging-distances (from home-sites) recorded for individual subjects were estimated and the utilisation of various prey-species was assessed. The data obtained from field observations, and other relevant records, were combined in order to gain a general overview of the daily activity patterns of the snakes.

1.2 THE STUDY AREA

As previously mentioned, *N.a. humphreysi* occurs in most areas of south-eastern Tasmania (Fig.3); consequently, selection of a suitable site for field-investigations was determined by two considerations, specifically the relative abundance of snakes in a given locality and facility of access. The Lake Sorell-Lake Crescent area (Figs.3 & 4) was considered eminently suited for the purposes of this study, because it is relatively isolated, supports a large population of snakes and its situation did not render costs of travel and transport prohibitively expensive.

The lakes are situated on the eastern perimeter of the Central Plateau of Tasmania, at an altitude of 800 m. Climatic data obtained for the area are summarised in Table 1. Mean annual rainfall is 557 ml (in 140 rainy days); the mean maximum temperature is 16.5°C and the mean minimum temperature is 3.8°C. The general climate of this region can be described as relatively dry throughout summer and winter, but wet in the early spring. Summer temperatures are mild, whereas winter temperatures are cold, often with overnight frost. The area is, in fact, usually subjected to frost and/or light snow falls in mid-winter.

Much of the lakes area is covered by sclerophyll forests alternating with grazing land scattered throughout the central and south-western sector (Fig.4). Marshes and bogs occur on the western shores of both lakes. Jackson (1972) stated that - "These natural lakes are probably all in part deflation lakes where the lake basin has been created by differential erosion of a sandstone body rimmed by dolerite". A diagrammatic section of the general area, adapted from Jackson (*op cit.*), is illustrated in Fig.5 and is considered to be representative of the vegetation-types and community-complexity of the area. The swamp vegetation was predominantly composed of *Triglochin* sp., the herbfield *Plantago* sp. and the tussock grassland *Poa billardiera*. The woodland and open woodland communities consisted mainly of *Leptospermum lanigerum* and *Eucalyptus pauciflora* respectively, whereas the dominant vegetation of open forest was *E. delegatensis* and *E. rodwayi*.

Grazing (by both cattle and sheep) occurred in the area and

TABLE 1 : CLIMATIC DATA OBTAINED IN THE STUDY AREA.

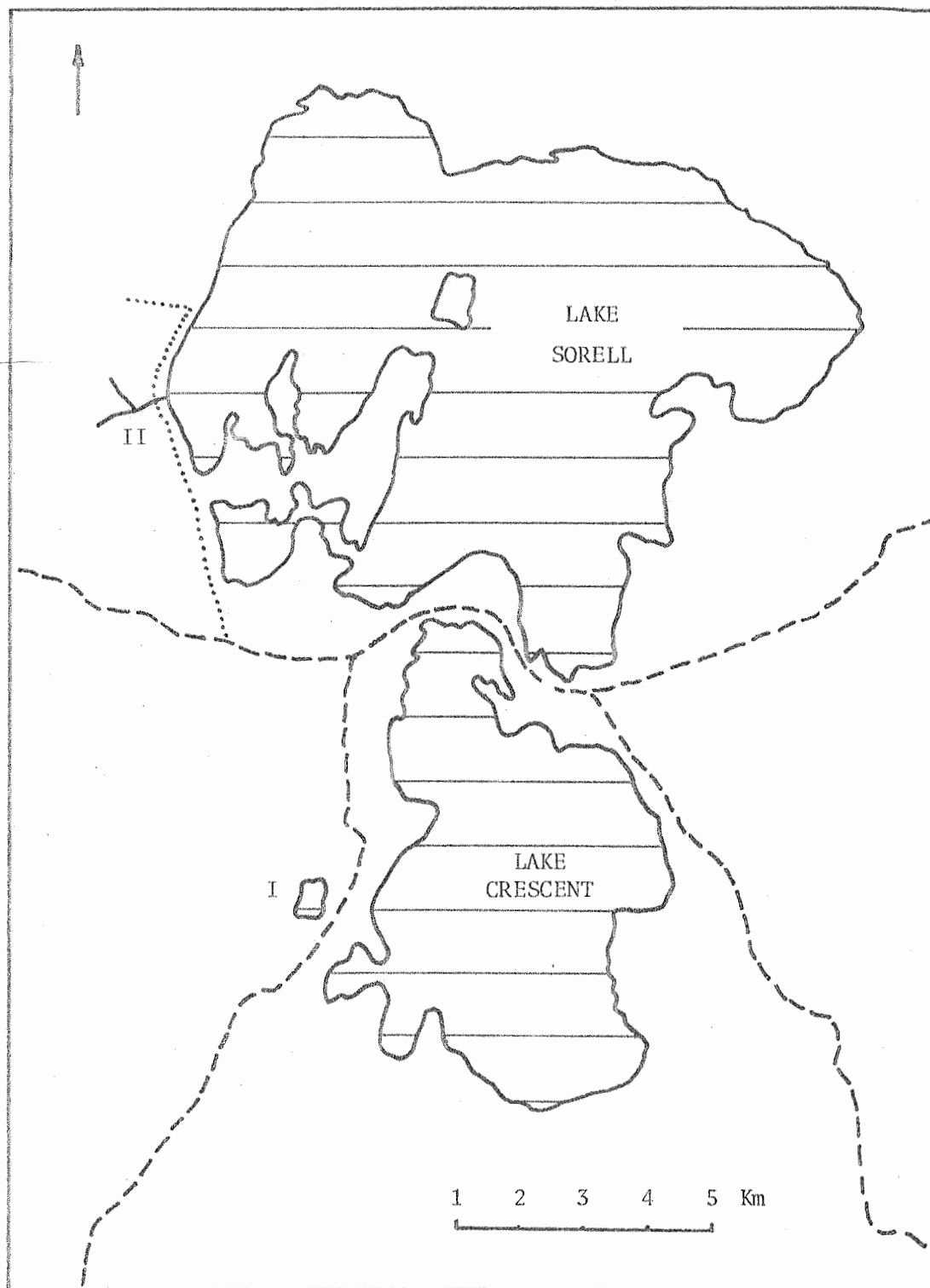
(a) Maximum and Minimum monthly temperatures ($^{\circ}\text{C}$).

	J	F	M	A	M	J	J	A	S	O	N	D
Max.	22.6	23.3	20.6	16.8	13.5	10.9	10.9	11.7	13.6	16.5	17.8	20.2
Min.	7.2	7.4	6.3	4.3	2.1	0.1	-0.2	0.6	2.2	3.3	5.5	6.5

(b) Monthly rainfall and days with rainfall recorded (mm).

	J	F	M	A	M	J	J	A	S	O	N	D
mm	37	41	37	51	45	45	47	47	45	56	53	53
Days	8	8	9	11	12	13	14	14	13	14	13	11

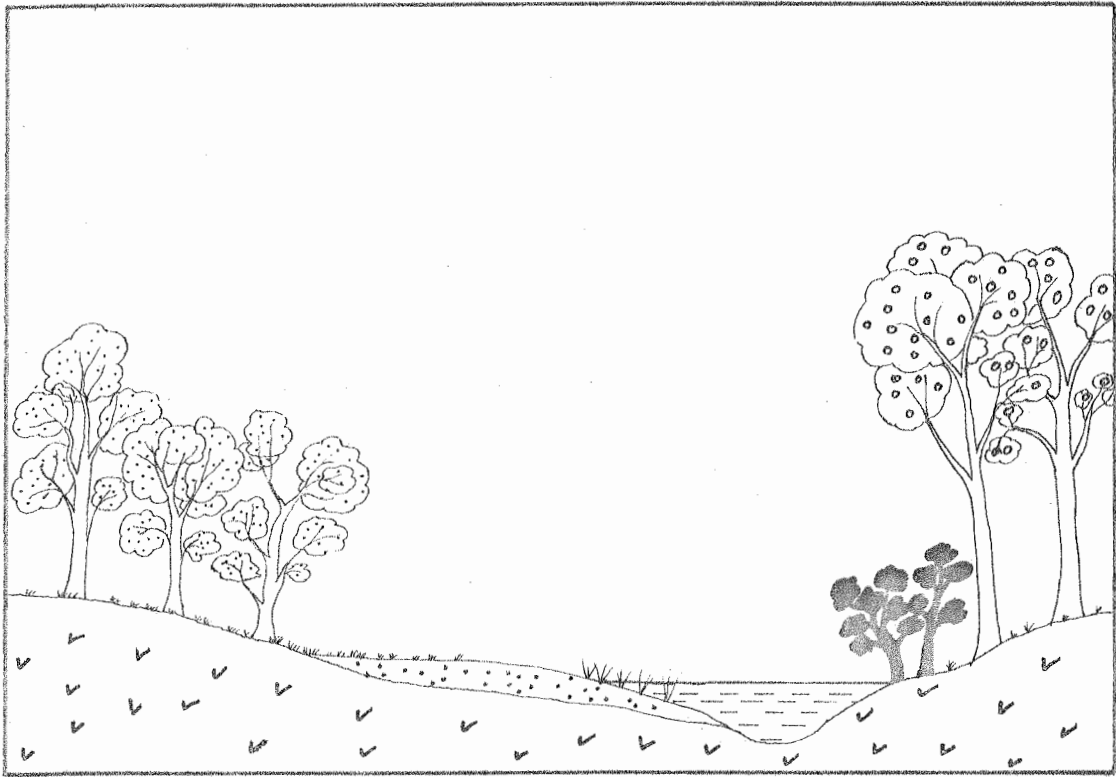
FIG.4 LOCATION OF THE PRINCIPAL STUDY AREA.



I (Site 1) - Brownwater Lagoon

II (Site 2) - Silverplains Creek

FIG.5 DIAGRAMMATIC TRANSECT OF THE STUDY AREA AT LAKE SORELL.
Modified from Jackson, 1972.



- Woodland



- Tall open forest



- Tussock grassland and herbfields



- Swamp



- Dolerite bedrock



- Sandstone

human recreational activity was conspicuous during late summer. Hunting (of wallaby and deer) was pursued and trout-fishing was regularly practised. Notwithstanding these activities, the numbers of *N.a. humphreysi* are usually high during summer in most localities within the area.

1.3 SPECIFIC STUDY-SITES

Although general observations of foraging activities and prey-species identification were made throughout the major study area, two specific sites were selected for collecting systematic records and for conducting detailed observations in natural conditions. This method of concentrating efforts in restricted localities permitted a more efficient utilization of observational opportunities than would have been achieved by casual gathering of information throughout the entire study area.

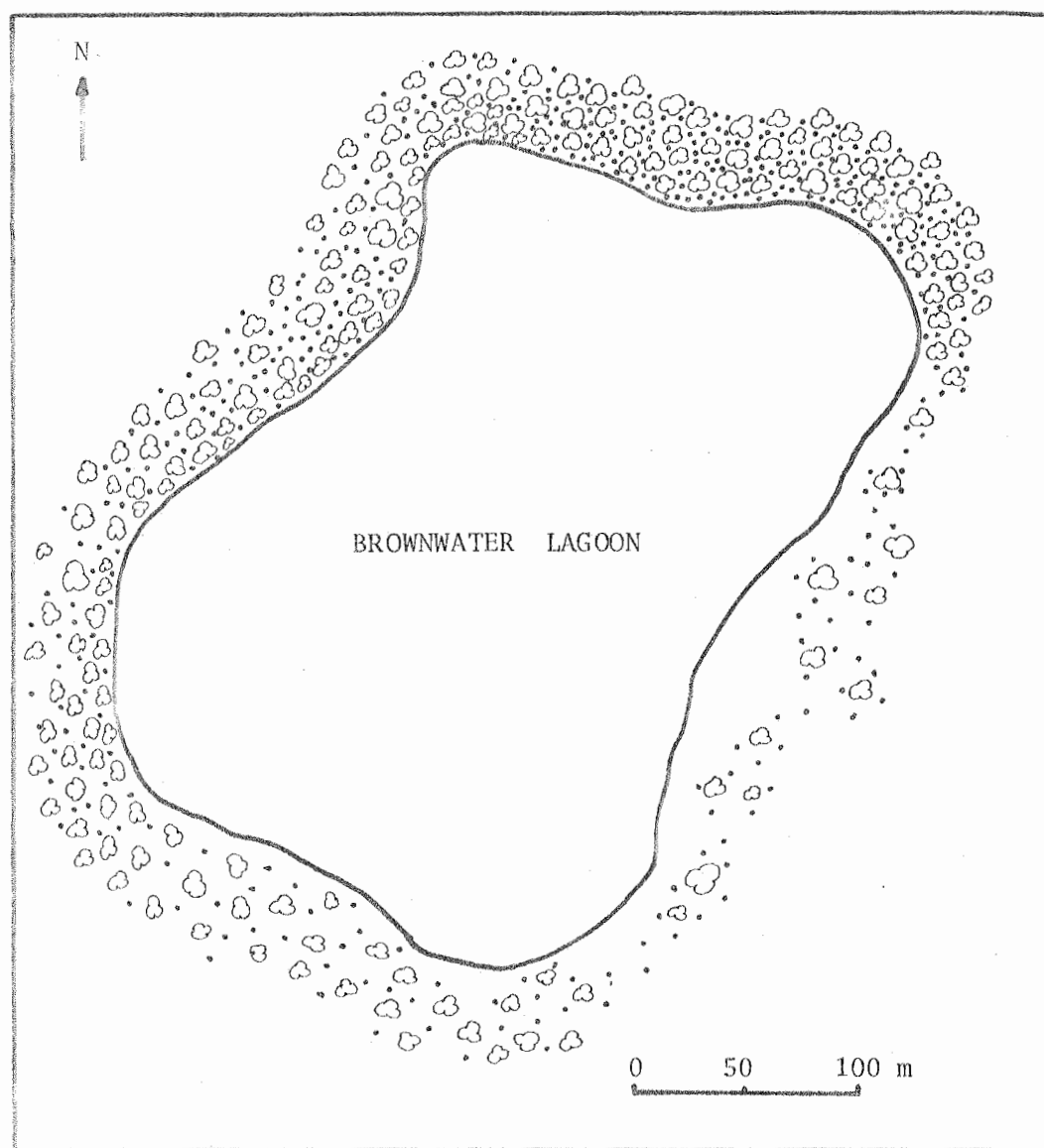
Study Site 1: Brownwater Lagoon

Brownwater Lagoon (Fig.4) is located at a distance of one km to the west of Lake Crescent, in open woodland interspersed with grazing pastures on the south-east banks. The lagoon proper is dry throughout the summer months and is utilised by sheep as grazing land. The dominant species of tree at this site is *E. rodwayi* and *E. pauciflora*. A crude estimate of the relative proportions of these species was 90% and 10% respectively. Small shrubs occurring in the area include *Helichrisum* sp., *Leucopogon hookeri*, *Cyathodes parvifolia* and *Bossiaea cordigera*. *Poa* grasses and *Plantago* sp. comprise the principal vegetation of the grasslands, whereas various species of sedges border the high-water line of the lagoon.

The relative densities of trees and small shrubs within a distance of 20 m to the high waterline, around the perimeter of the lagoon, are illustrated in Fig.6. The positions of prominent dolerite outcrops are indicated in Fig.7. These formations are extensively weathered and exfoliated boulders, protruding above the surface of the ground or are partly submerged within the soil.

The communities around the perimeter of the lagoon may be assigned to three distinct habitat-types. Firstly, the northern perimeter, having a denser growth of shrubs and mosses due to the "shading" effect of the tree canopy (Fig.8a). Secondly, the southern perimeter has less ground-level vegetation since it receives more direct sunlight than the northern perimeter. The prevailing conditions create a drier, more open, small-shrub community (Fig.8b).

FIG. 6 RELATIVE DENSITIES OF VEGETATION AROUND THE PERIMETER OF SITE 1 (BROWNWATER LAGOON).

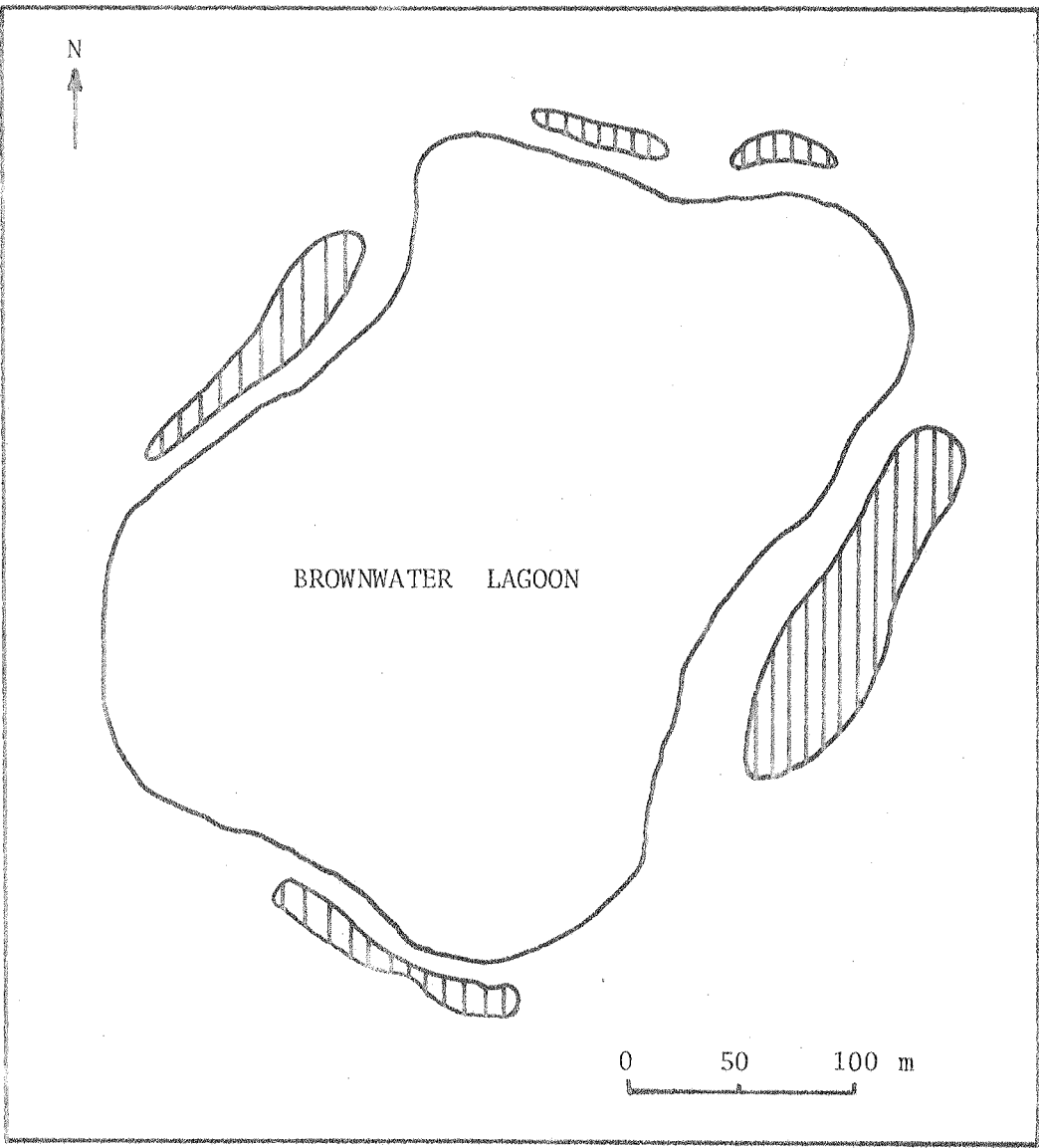



- Trees



- Shrubs

FIG.7 PROMINENT DOLERITE OUTCROPS AT SITE 1 (BROWNWATER LAGOON).



 - Dolerite outcrops

Clearing of the pastures has rendered the eastern perimeter more open, with comparatively little vegetation and high grazing pressures. The western perimeter may be described as a transitional vegetation between the northern and southern perimeters.

Study Site 2: Silverwater Creek

Silverwater Creek (Fig.4) collects a series of drainage canals from grazing pastures and open woodland, and flows into the western shore of Lake Sorell. The creek is dry in the summer but has abundant water during most of the winter and spring, when it is used for breeding of Lake Sorell trout. The dominant tree species at this site is *E. pauciflora*, accompanied by stands of *Leptospermum lanigerum*. Several species of shrubs are present, including, *Leucopogon hookeri*, *Bossiaea cordigera* and *Cyathodes parvifolia*. The grassland is composed of *Poa* sp. and the herbage is mainly comprised of *Plantago* sp.

Fig.9 illustrates the relative densities of vegetation within 20 m of the banks of the creek for a distance of 600 m. The southern aspect of the creek is heavily grazed by both sheep and cattle, whereas the northern side is well-forested, particularly around the marshy area. Although dolerite exfoliations and boulders flank the creek (Fig.10), there are no conspicuously large outcrops such as those evident at Site 1.

FIG.8 CHARACTERISTIC VEGETATION AT BROWNWATER LAGOON (SITE I)

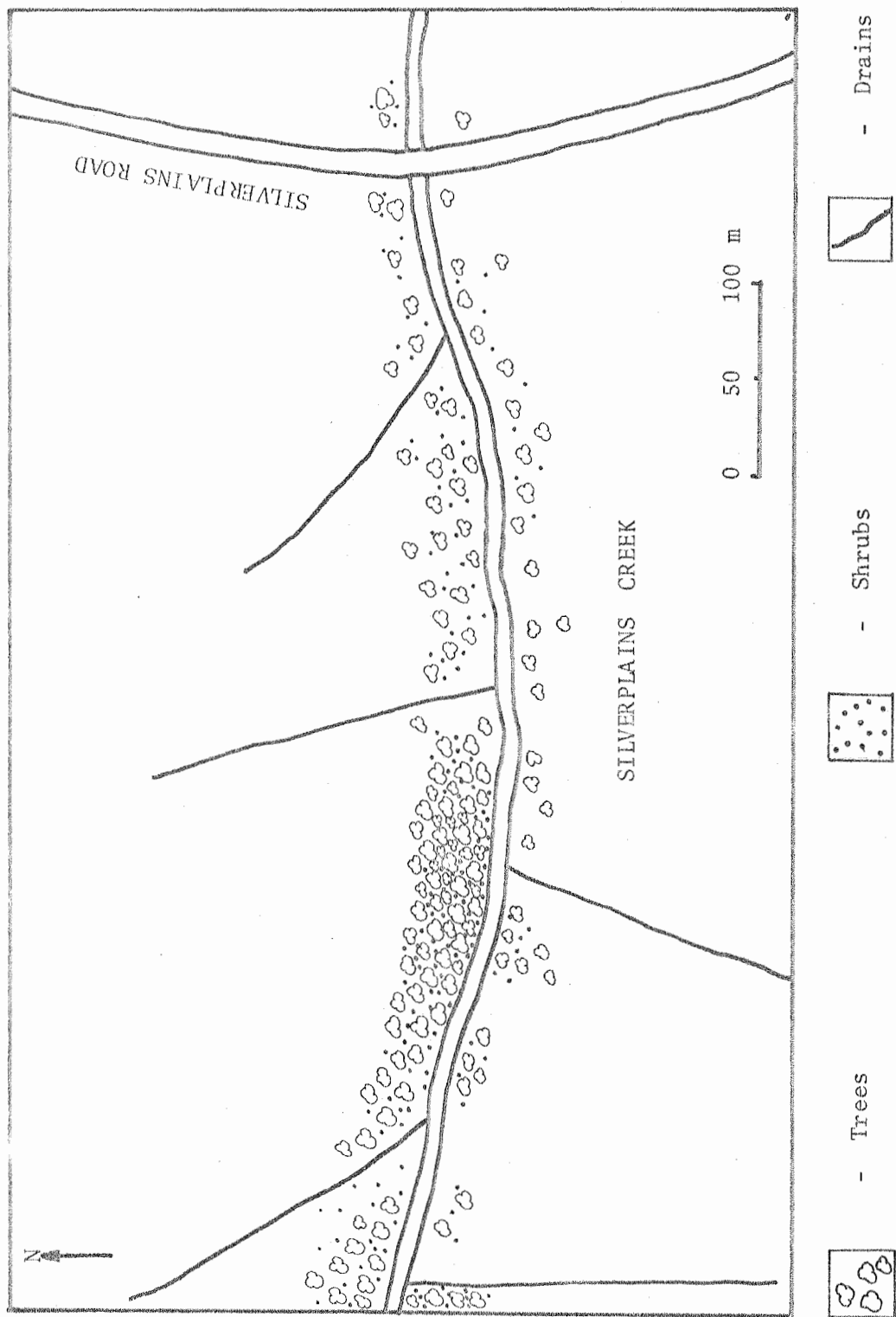


(a) The northern perimeter.



(b) The southern perimeter.

FIG.9 RELATIVE DENSITIES OF VEGETATION ALONG SITE 2.



1.4 MATERIALS AND METHODS

It was anticipated that observation and capture of *N.a. humphreysi*, and the recording of relevant data, would be a prolonged and time-consuming procedure; it was further expected that the observer, or observers, would be required to move over a considerable amount of terrain during each field-exercise. For this reason, the use of complex or heavy recording-equipment was considered impractical and instead light-weight and easily employed equipment was selected. Since the nearest available snake-bite anti-venine facilities were situated at a distance of at least two hours (by road) from the study-area, actual handling of the snakes, e.g. for the purposes of recording body-temperatures, was limited to occasions when suitably competent field-assistance was available. Safety precautions of this type are considered essential when handling large and potentially dangerous elapids under field-conditions.

Information about foraging and basking behaviour, as well as prey species data (concerning the availability of prey-species) were collected by the author, unaccompanied by assistants. Capture and observation of the snakes was accomplished by systematically searching a twenty m area around the perimeter of both study-sites; specifically within twenty m of the lagoon edge and twenty m on either side of Silverplains Creek. Attempts at examining a larger area would have demanded excessive amounts of time and effort, unsuitable for the purposes of this study.

Capture of the subjects was achieved by approaching them rapidly and restraining the anterior end of the body against the substrate, using a capture-brace. This apparatus consisted of a one m wooden handle attached to a metal fork, across which was fixed a two cm-wide piece of rubber. The snake was then held close to the surface of the ground at the site of capture (Fig.11) while its body temperature and other relevant measurements (e.g. dimensions) were recorded. The animal was subsequently transferred to a sack for the purpose of further examination. After recording the pertinent information, snakes were released at the site of their capture and permitted to return to their home-sites or to continue their activities.

FIG.10 CHARACTERISTIC VEGETATION AT SILVERPLAINS CREEK (SITE IIa).



FIG.11 THE METHOD EMPLOYED IN RESTRAINING SUBJECTS WHILE MEASURING OESOPHAGEAL TEMPERATURES.



1.4.1 The Protocol-sheets Used in the Field-investigation

Numerous environmental variables may have potentially important effects on the activities of thigmothermic squamate reptiles in natural conditions. The factors selected for detailed assessment in the present study are those considered by the author to be the most relevant in terms of effective thermoregulation, the maintenance of optimal body temperatures and general adaptability to the environment by a "cold-climate" elapid. A preliminary evaluation of the relevant parameters, as well as methods of recording on field protocol-sheets (Table 2) may be summarised as follows:

(a) Identification of Individual Subjects

It was initially intended to investigate the movements of individual snakes, for the eventual purpose of assessing population parameters, by recording the locations of successive re-captures, after marking each captured individual. Marking was accomplished by painting a Roman numeral on the dorsal surface of the body, approximately fifteen cm from the anterior border of the snout, while the snake was being held to the ground. The material employed for the purpose was a commercially-prepared white enamel "touch-up" paint manufactured by Selleys Australia Ltd.

Although periodic sloughing of the skin may be expected to obliterate the mark, this was considered an efficient and easily recognisable identification technique, suitable for short-term investigations. It is important to note that an alternative method, scute-clipping, is a relatively durable means of achieving the same end, but the resultant marks are quite cryptic and in general the marked animal has to be re-captured and extensively manipulated in order to be accurately identified. Since estimates of foraging distances need only be accomplished by observation at a distance, rather than by actual capture, the method employed in the present study was suitable for use by a solitary investigator.

(b) Posture

The importance of shuttling (whole body movements in relation to heat sources) and postural changes, for example, elevation and/or alterations of the normal configuration of the body during thermo-

TABLE 2. PROTOCOL SHEET USED IN FIELD-INVETIGATIONS (See Section 1.4.1 for Conventions).
Where no posture is given, the animal was actively foraging.

Subject	Posture	Per Cent Cloud-cover	Time of Capture	Distance to Home (m)	Activity-status F B	Ta C°	Ts C°	Tb C°	Length (cm)	Weight (gms)	Sex	Habitat- type
1	Looped	98	9.10	1.5	x	15.5	21.0	19.5	151	1250	M	1
2		95	9.40	6	x	14.0	19.5	18.5	129	1050	M	2
3		90	10.00	3	x	14.5	19.0	22.5	126	1050	F	4
4	Looped	100	11.35	0.5	x	15.0	24.0	24.0	126	800	M	4
5	Looped	100	11.55	-	x	15.5	24.5	22.0	130	850	F	4
6	Coiled	100	2.10	0.5	x	17.0	24.5	27.0	115	500	M	4
7		90	2.40	0.5	x	21.0	28.5	29.5	103	400	M	2
8		80	2.55	10.0	x	17.5	28.0	28.5	132	900	M	4
9	Coiled	50	4.15	0.5	x	21.0	31.0	27.5	141	1000	M	3
10		50	1.30	0.5	x	19.0	31.0	24.5	138	1400	F	1
11		40	4.50	15	x	21.0	29.5	29.0	140	1550	F	3
12		50	9.20	0.5	x	24.0	31.5	29.0	136	1150	F	3
13		40	10.20	20	x	23.0	26.0	27.0	151	1200	M	4
14		30	11.15	4	x	28.0	35.0	31.0	116	600	F	1
15		20	11.45	7	x	30.0	39.0	30.5	140	900	M	1
16	Coiled	15	12.50	0.5	x	32.0	35.0	26.5	141	1550	F	3
17		60	1.05	-	x	30.0	31.0	27.0	145	1550	F	2
18		0	10.45	1	x	19.0	12.0	26.0	140	950	F	4
19		0	2.40	-	x	21.0	30.0	29.0	130	850	M	4
20	Coiled	30	11.35	0.5	x	13.0	17.0	25.0	135	1400	F	1
21	Coiled	60	1.50	0.5	x	11.0	13.0	25.0	125	1050	F	4
22		0	1.50	-	x	17.0	28.0	29.0	140	1150	F	4
23		30	11.0	2	x	20.0	26.0	30.0	112	450	F	3
24		40	11.20	0.5	x	21.0	22.0	31.0	136	850	M	1
25		30	11.55	-	x	20.0	22.0	26.0	108	650	F	5
26	Coiled	15	1.30	1	x	24.0	26.0	25.5	141	1600	F	5

regulatory activities, has been recognised by several investigators, (Heatwole 1976 and 1979) and is considered to be an important, albeit subtle, category of behavioural elements in the daily activity of squamate reptiles. Records of the postures of individual subjects were based on field sketches of the relevant conformations of the body, prepared before the subjects were captured. Shuttling is discussed in more detail elsewhere.

(c) Per Cent Cloud-cover

The effects of cloud cover, particularly in relation to activity-status, have been documented by Gibson and Falls (1979) and are generally regarded as having a controlling influence on emergence (from home-sites) and other activity-patterns. In the present study, the percentage of cloud-cover was estimated simply by direct observations made at the time of capture of each individual subject.

(d) Time of Day

Various species of *Notechis* occurring in continental Australia, as well as other large elapids, have been shown to be diurnal, crepuscular and in some cases, nocturnal (e.g. Gow 1976). The ability of a predator to forage for food during both light and dark periods may provide an indirect indication of the utilization of potential prey-species. For example, a crepuscular or nocturnal predator is able to feed on animals not normally active in daylight and therefore not available, in an active state, to diurnal predators. This is of particular importance in the feeding habits of Australian elapids, since prospective prey-species, such as frogs and small native mammals, are generally crepuscular and/or nocturnal.

During daylight periods, the activity levels of *N.a. humphreysi*, as those of other reptiles, is a function of the availability and duration of exposure to solar radiation, as well as the intensity of radiation. By recording time of capture, it is possible to detect the occurrence of circadian rhythms in the activities of the animals at various stages of the seasonal cycle.

(e) Proximity to Home-site

The distance an animal moves from its home-site during daily

activity-periods may provide some indication of its habitat-usage and expenditure of energy during foraging and/or reproductive activity. Shine (1979) was able to determine that two specimens of *N.s. scutatus* had approximately rectangular activity-ranges, comprising 0.75 and 0.77 hectares, respectively. Shine further established that both *N.s. scutatus* and *A. superbus* are very sedentary, whereas *P. porphyriacus* moves more extensively throughout its habitat.

N.a. humphreysi may be expected to show a similar activity-range to that of *N.s. scutatus*. In order to estimate this, the distance between the sites where individual subjects were captured and their known home-sites were recorded. In some instances, animals did not return to a "permanent home-site" after they were released, but continued to forage or took refuge under temporary cover. In situations of this type, distances were not recorded. Records of data pertaining to distances were combined with data relating to observations of foraging behaviour to obtain a tentative estimate of activity-ranges. The concept of "permanent home-site", or hibernacula, is discussed below (Section 1.5.1).

(f) Activity-status

The term activity-status refers to two basic categories of activity observed in the subjects, i.e. whether they were captured while basking or while actively foraging. In each recorded episode, subjects were observed for two minutes prior to capture, in order to establish which of the two categories of behaviour were applicable. The activity-status of the animals was considered important in relation to maintenance of their favoured body-temperatures, their circadian rhythms, and their general daily activity-patterns.

(g) Temperatures

The precise relationships between ambient, or air-temperatures (T_a), substrate temperatures (T_s) and body-temperatures (T_b), are highly variable among squamate reptiles occurring in different parts of the world. As *N.a. humphreysi* is a thigmothermic squamate, it was expected that body-temperatures would be more closely related to substrate-temperatures than to ambient-temperatures. Furthermore, *N.a. humphreysi*, being a cold climate squamate was expected to be active at lower temperatures (both ambient and substrate), than

snakes of similar size and habits inhabiting warmer climates.

Ambient temperatures were recorded by placing a glass-rod thermometer 30 cm above the substrate for a period of two minutes. Substrate temperatures were recorded by placing the thermometer on the substrate and shading it from direct radiation for two minutes. All estimations of temperatures extraneous to the subjects themselves were made after the body temperatures of the snakes had been recorded.

Body-temperatures were recorded by inserting the thermometer into the oesophagus of the subject (Fig.11) until the temperature had stabilized. Temperature stabilization was reached in less than two minutes. Oesophageal temperatures were chosen to represent body temperatures because of the rapidity and ease at which the procedure could be performed. It was considered important that body-temperatures be recorded as quickly as possible, because of the possibility that they may change due to activity during restraint. Attempts to record cloacal temperatures proved to be more difficult and time-consuming.

(h) Body Length

Total body-lengths (from the tip of the snout to the tip of the tail) of individual subjects were recorded at the time of capture, while animals were held close to the substrate. Although snout-vent lengths have previously been used (Worrell 1964 and Cogger 1979) as body measurements for snakes, it was considered, in the present study, that total body-length was more relevant in terms of thermoregulation. Measurements of length were used to examine the relationship between that parameter and body temperatures.

(i) Body Weight

Each subject was weighed by placing it in a sack and attaching a spring balance to the latter, the weight of the sack was then subtracted from the estimated total. The information so obtained permitted investigation of length-weight relationships as well as body temperature-weight relationships.

(j) Sex

In Australian elapids the sex of an individual may be determined by the characteristics of the posterior of the body, from a dorsal aspect. In females the position of the cloaca is distinguishable by a constriction of the proximal end of the tail. The tail in females being more "conical" than in males which have a comparatively longer tail and do not exhibit a post-cloacal constriction when examined from a dorsal aspect. The sex of all subjects, in the present study, was determined at the time of their capture. Sex-related differences with respect to thermal ecology, length, weight and other factors were subsequently examined.

(k) Habitat-type

For the purpose of assessing habitat-utilization, five categories of distinctive habitat types were established in the study area. These are as follows:

i. Rock-outcrops . This category is used to indicate that subjects were located in an area characterised primarily by the presence of dolerite exfoliations and boulders.

ii. Fallen timber . This category includes naturally fallen trees, as well as those felled during clearing operations by landowners operating in the area. The fallen trees occurred in small clumps but also single, throughout the study area.

iii. Open grassland . Since the area was grazed by domestic livestock (both sheep and cattle), a considerable portion of each study-site consisted of paddocks or open grassland.

iv. Small rock-outcrops occurring within grassland . In much of the study-area, smaller rock outcrops occur in cleared or partially cleared land. These occurred in both study-sites.

v. Dense vegetation . This category is characterised by dense growths of shrubs, illustrated in Fig.8a. Habitats of this type were restricted to a few localities within the study-area. Fig.8a is a "typical" dense vegetation habitat, whereas Fig.8b was classified as small rock-outcrops occurring within grassland (habitat type iv).

1.4.2 Effect of Recordings

The time required to record the data on field protocol-sheets never exceeded ten minutes from the time of capture to the time of release of the subjects. The only apparent effects of the techniques employed was slight bleeding from the mouth, in eight of the subjects, caused by biting the thermometer while oesophageal temperatures were recorded. The adverse consequences appeared to last for short periods, as four of the subjects exhibiting them were observed to re-emerge from their home-sites within two hours of recordings.

1.4.3 Direct Observations in the Field

During the period February 1st - May 20th, an aggregate of 150 hours were devoted to direct observations on the activities of *N.a. humphreysi* in the field. Observation-periods were variable in duration, (dawn to dusk; mornings only; and afternoons only). Twenty of the 150 h were spent in nocturnal observations which were conducted by flashlight for a period of two h after dark. Generally, observations were made at a distance of at least 5 m from a given subject. This ensured that the subject was unaware of the presence of the observer. The equipment used during observations consisted of 7x50 field glasses and a 35mm camera, in addition to protocol sheets and other recording devices.

On several occasions the subjects being observed exhibited behaviours not consistent with "normal" foraging activity. These consisted of moving off at high-speed or, turning toward the observer in an agonistic posture, as shown in Fig.1. In both instances it was assumed that the observer's presence had been realized by the snake and, subsequently, observation was terminated.

Observation procedures involved systematically searching a specific study site until a snake was discovered. Thereafter the animal's activity status was recorded for varying durations. Generally one to two h were sufficient until the animal was lost from sight in its home-site or in vegetation. These observations, although tedious and time-consuming, proved to be of considerable value in assessing such behavioural events as foraging activities, and

thermoregulatory behaviour, as well as providing information about activity-ranges.

Estimates of the diversity and density of possible prey-species were obtained by random sampling of potential sites of their occurrence, for example, logs, rock, etc., at each study-site. Analysis of the contents of the digestive tract of snakes was restricted to road-kills in the study-area. This ensured that sufficient numbers of snakes were available for in-vitro investigations at the completion of the field study.

An investigation into the occurrence of parasites was carried out in the field and within the laboratory. A short-list of the parasites found to be utilizing *N.a. humphreysi* as a host is given in Appendix 'A'. The recordings are not intended as a quantitative analysis but simply a record of occurrence.

1.5 RESULTS

1.5.1 The Permanent Home-site Defined

During the period when systematic recording of data was undertaken and direct observations were made in natural conditions, it was noted that *N.a. humphreysi* utilized several distinctive types of home-site, each having characteristic features. The precise nature of a home-site appeared to be determined by the type of habitat currently utilized and varied from burrows in the soil to hollows beneath fallen timber and within rock-crevices, as well as under rocks. A "typical" rocky habitat home-site is shown in Fig.12a and diagrammatically illustrated in Fig.12b.

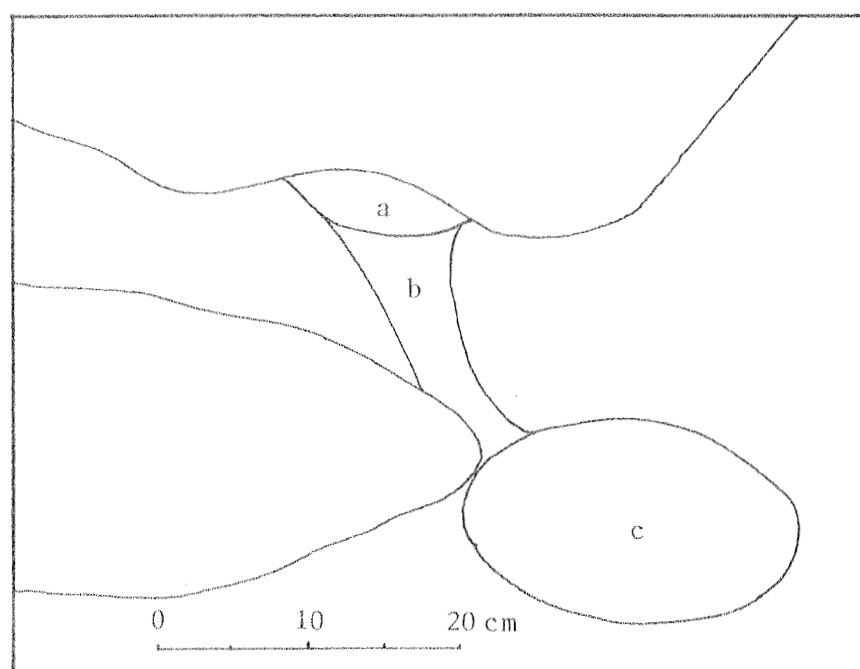
The characteristic features of the permanent home-site may be described as follows:

- a. The entrance of the home-site. Regardless of the nature of the home-site, the entrance was always clearly defined as an elliptical or circular opening of approximately five to ten cm in diameter. The entrance was clear of vegetation or debris in all recorded instances; the surrounding vegetation, in the immediate vicinity of the entrance, was separated and/or flattened to the substrate, presumably facilitating ease of entrance.
- b. Short trail. A clearly defined area of flattened vegetation immediately outside the burrow entrance was characteristic of all permanent home-sites. This short trail always extended by the most direct route from the entrance of the home-site entrance to the basking pad.
- c. The basking pad. An elliptical or circular area of flattened vegetation, varying in diameter from twenty to thirty cm was situated in close proximity to the entrance of each home-site. Post-emergence basking was invariably practised on this area of the substrate. In the majority of instances (36 of 50 home-sites examined = 72%) a larger area of flattened vegetation occurred within a short distance of the post-emergence basking pad. Pre-foraging basking was typically performed in these localities. The concepts associated with post-emergence and pre-foraging basking-behaviour are discussed below.

FIG. 12 TYPICAL PERMANENT HOME-SITE SITUATED UNDER A DOLERITE BOULDER.



(a) Appearance (surface view).



(b) Diagrammatic outline of the principal features.

a) Entrance of the homesite, b) short trail, c) basking pad

A total number of 50 home-sites were examined in detail and the only variations noted with respect to the above characteristics occurred where a home-site was either located in large rock-outcrops or within piles of timber. In these situations basking was performed on the rock or timber surfaces and few or no signs of trails or basking-pads were evident. Of the 50 home-sites examined 40 were within or beneath rocks, representing an 80% preference for rock habitats.

1.5.2 Activity Range and Distribution

During the period of active field-study and recording, no subject was physically captured and recorded on more than a single occasion. However, eight subjects (i.e. subjects number three, five, seven, eleven, twelve, fourteen, twenty and twenty four) were sighted on at least one occasion after the episode of their initial capture and marking; subjects eleven and twelve were observed on two occasions subsequent to their first capture. The distance each of these animals were found from the home-sites, identified at the time of their initial capture, are listed in Table 3. In the case of subject five, the distance recorded on first sighting refers to the distance from the original location of capture rather than from the home-site, since the location of the latter was unknown.

The maximum distance any subject was found from the initial home-site was 50 m (subject eleven) and the minimum recorded distance was 0.5 m or less. Subjects seven, eleven and twelve were observed to occupy different home-sites than those identified at the time of their original capture. These three animals were seen returning to, and emerging from new home-sites twenty, fifty and ten m, respectively, from the home-sites they were first noted to use.

In the course of the direct observation periods a total of twenty individual snakes were observed to leave their home-sites, forage and then return to the home-sites. During other sessions of observation, other animals were either sighted after they had left their home-site (i.e. already foraging when first located) or were lost from view during the course of observation. Data so collected was used for foraging behaviour analysis and not for home-range analysis.

Table 4 shows the duration of time each subject was observed, as well as the estimated distance it moved during foraging-activity. Duration of actual foraging, by each individual, is also given. In episodes characterised by distance moved equalling zero, animals were observed while basking only. The behaviour of these snakes is further discussed below (Section 2.1). The data relating to distances moved are not based on actual, recorded distances from the home-sites but to the distances the animals are known to have travel-

TABLE 3 : DISTANCE FROM ORIGINAL HOME-SITES (m).

Subject	Initial Capture	1st Sighting	2nd Sighting
3	3.0	0.5	-
5	-	2.0	-
7	0.5	20.0	-
11	15.0	30.0	50.0
12	0.5	3.0	10.0
14	4.0	0.5	-
20	0.5	10.0	-
24	0.5	0.5	-

led in the course of their foraging activities. In some instances the snakes foraged in a circular pattern around the home-sites or in various directions along the creek-bed. Foraging behaviour is described in more detail elsewhere (Section 2.2).

As the data presented in Table 4 demonstrates, the maximum distance any subject was observed to move was ca. 50 m but the mean distance travelled by all snakes was 19.2 m. These data also show that *N.a. humphreysi* may move as short a distance as four m during a bout of foraging activity. The mean duration of foraging was 2.48 h (based on records obtained for twelve subjects); the maximum duration was four h and the minimum one-half h.

The maximum distance at which a snake was located from its home-site was twenty m (subject 13, Table 2), the maximum distance covered by any animal during foraging-activities was 50 m (subject 36, Table 4), the maximal duration of foraging (four h) was also recorded for the same subject. Observations made on subjects seven, eleven and twelve clearly indicate that these animals did not necessarily confine themselves to a single home-site but were, in fact, capable of utilizing several sites during one season.

The spacial distribution of the animals captured and recorded at Study Site 1 (Brownwater Lagoon) is illustrated in Fig.13. The distribution of the subjects captured and examined at Study Site 2 (Silverplains Creek) is shown in Fig.14. The dispersion of the snakes occurring along the perimeter of Brownwater Lagoon appears to be clumped whereas that of the population of Silverplains Creek is more random. Male snakes were clustered together at the southern edge of Brownwater Lagoon but both male and female individuals appeared to be evenly distributed along Silverplains Creek.

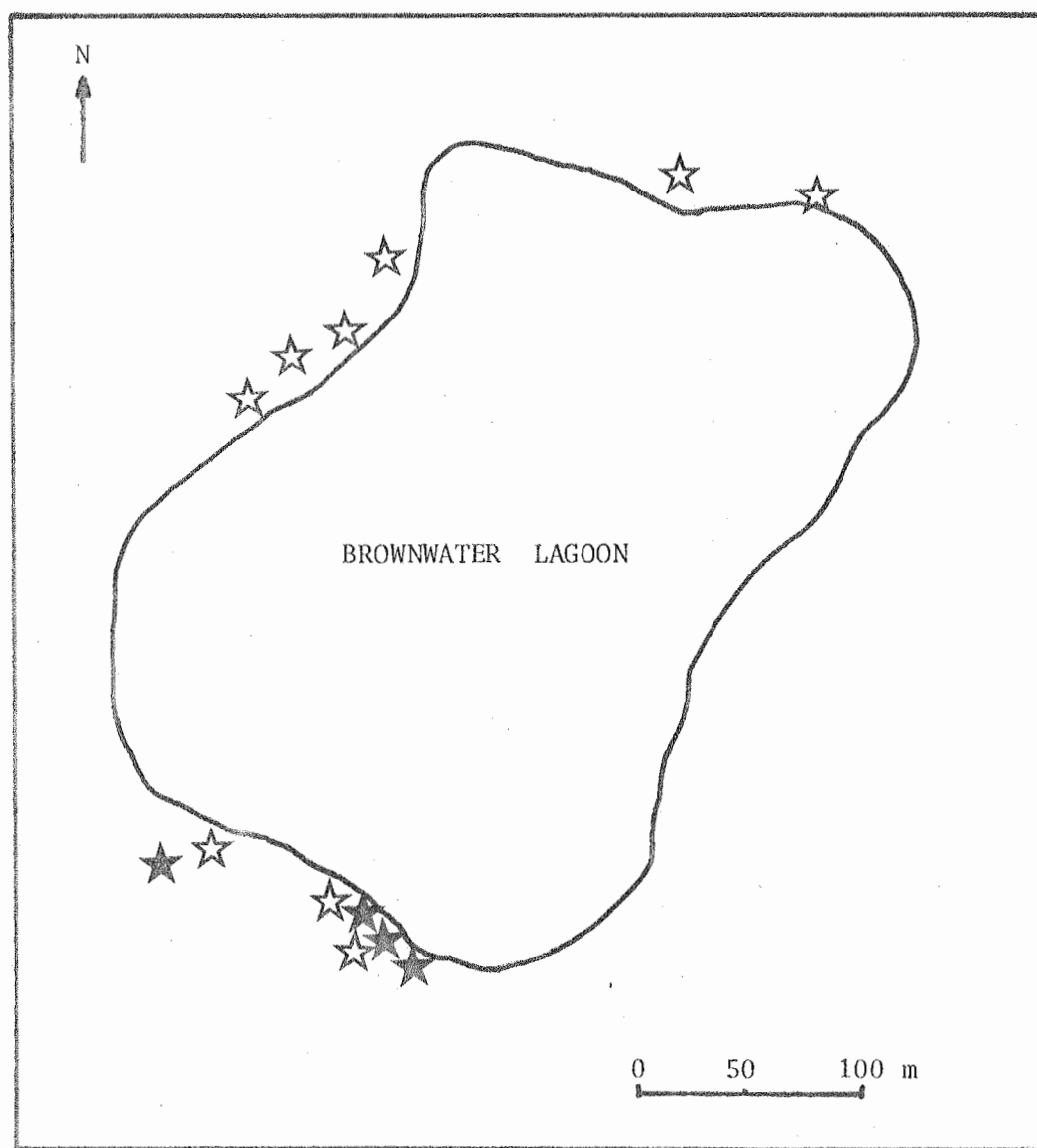
TABLE 4 : FORAGING RANGES.

Subject	Duration of Observations (h)	Distance Moved (m)	Duration of Foraging (h)
7	1.5	10	1.0
12	0.5	0	-
27	1.5	30	1.25
28	2	25	1.0
29	2	10	0.75
30	2	0	-
31	1	20	0.75
32	1	0	-
33	1	0	-
34	0.75	4	0.5
35	2.5	10	2.0
36	5	50	4.0
37	1.5	36	1.25
38	0.5	0	-
39	2	5	1.0
40	2	20	0.75
41	3	20	1.0
42	1	0	-
43	1.5	0	-
44	0.5	0	-

N = 20

 Σ 32.75 \bar{X} 19.2 \bar{X} 2.48

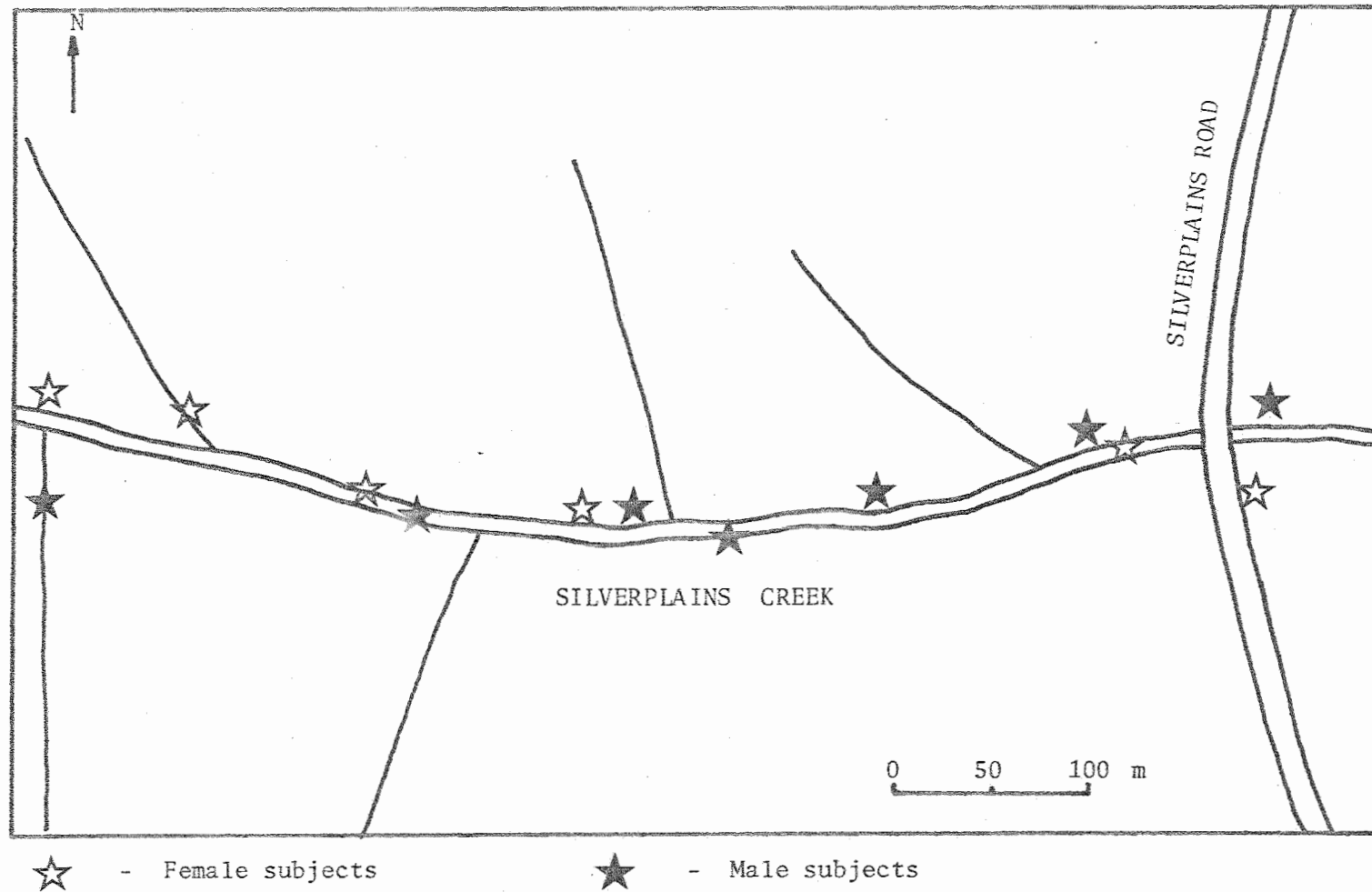
FIG.13 DISTRIBUTION OF *N.A. HUMPHREYST* CAPTURED AT SITE 1.



☆ - Female subjects

★ - Male subjects

FIG.14 DISTRIBUTION OF *N.A. HUMPHREYSI* CAPTURED AT SITE 2.



1.5.3 The Effects of Cloud-cover on General Activity and Body Temperature

In an attempt to analyse the information relating to the effects of cloud-cover, estimates of percentage cloud-cover were arbitrarily assigned to ten categories. Fig.15 is based on the relationships of these to the actual numbers of animals observed to be active, as well as the relative proportion (percent) active animals related to each class. Although there was evidence of minor peaks in activity (the number of active animals corresponding to the 21-30% and 91-100% categories) a chi-squared test applied to the data yielded the value of 8.6 ($df=9$) and the differences were not significant ($P > 0.5$, 0.3). The implicit null hypothesis that cloud-cover has little or no effect on activity of *N.a. humphreysi* is therefore sustained, because the critical χ^2 ($P > 0.5$) would have been 16.9. The absence of active animals corresponding to category 61-70% is probably of little significance and may be purely a consequence of the random sampling method employed during the observations.

The data presented in Fig.16 illustrates the relationship between individual cloud-cover classes and the mean body-temperatures of the animals recorded for each of the latter. Although a slight peak in body-temperature appeared to occur in subjects assigned to the 41-50% class and thereafter a slight decline, the chi-squared test yielded the value of 28.2 ($df=9$). This was significant ($P < .01$) when the observed values (Table 5) were compared with the expected class mean of 23.3. Furthermore, regression analysis of the body-temperatures in relation to estimated percentages of cloud-cover (Fig.17) suggests that body-temperatures declined with increasing cloud-cover.

Consequently, the variations in body-temperatures about the expected mean that occurred throughout all categories of cloud-cover, may be considered significant and a moderate decrement in body-temperatures with increasing cloud-cover may be surmised to occur ($r = -0.53$).

The above results indicate that general activity-levels of *N.a. humphreysi* are, at most, loosely associated with differences in cloud-cover and this species may be active under clear, cloudless

FIG.15 THE NUMBER AND PROPORTION OF SUBJECTS OBSERVED TO BE ACTIVE IN RELATION TO PER CENT CLOUD-COVER.
 Barred columns illustrate numbers and solid bars represent proportions (per cent) of active subjects.

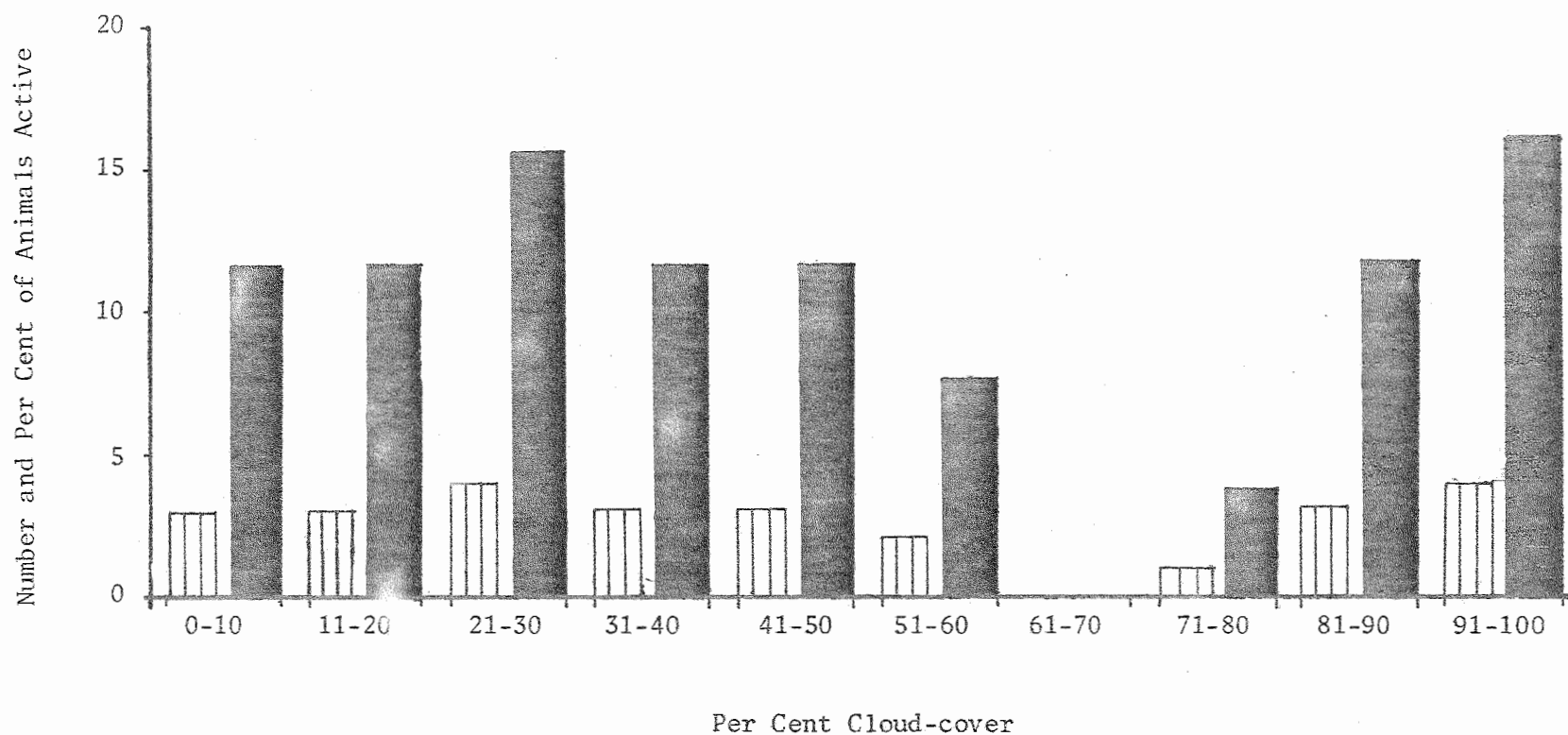


FIG.16 BODY TEMPERATURES OF SUBJECTS IN RELATION TO PER CENT CLOUD-COVER.
Mean values ± 1 standard error are shown.

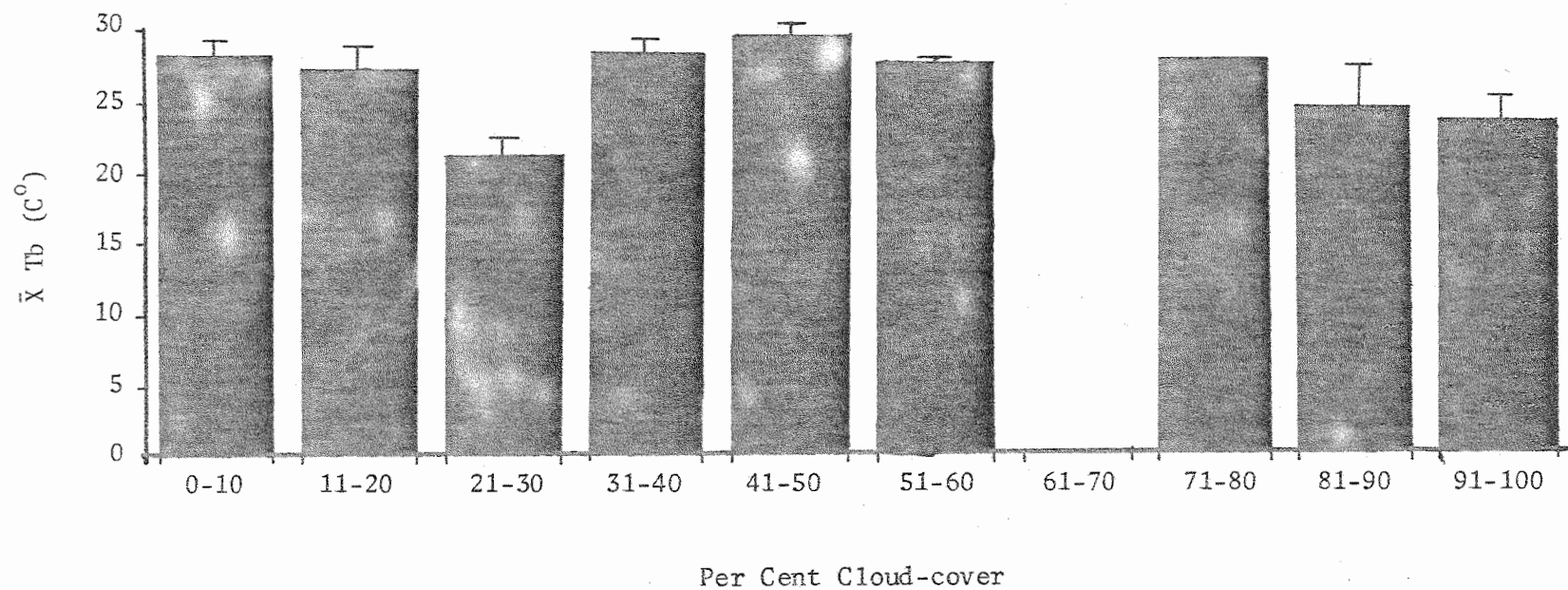
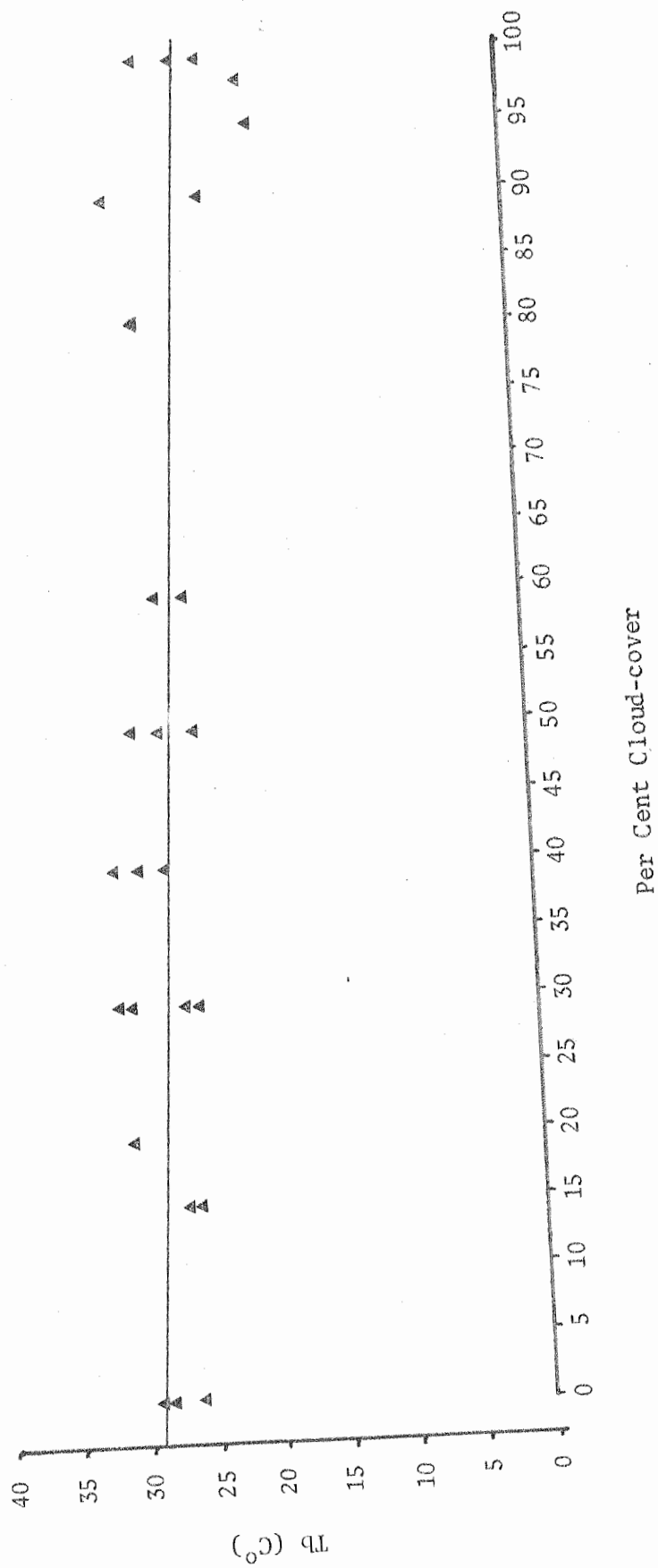


TABLE 5 : ACTIVITY AND BODY-TEMPERATURE IN RELATION TO CLOUD-COVER.

% Cloud-cover	No. of SS	% of SS	\bar{X} B+ C ^o
0- 10	3	11.5	28.0
11- 20	3	11.5	27.5
21- 30	4	15.3	28.0
31- 40	3	15.4	29.0
41- 50	3	11.5	27.0
51- 60	2	7.7	26.0
61- 70	0	0	0
71- 80	1	3.8	28.5
81- 90	3	11.5	23.5
91-100	4	15.3	23.1

FIG.17 INDIVIDUAL BODY-TEMPERATURES IN RELATION TO PER CENT CLOUD-COVER.



skies, as well as completely overcast conditions. Although cloud-cover did not appear to affect activity, it did exert some effects on body-temperatures; these slightly decreased as cloud-cover increased.

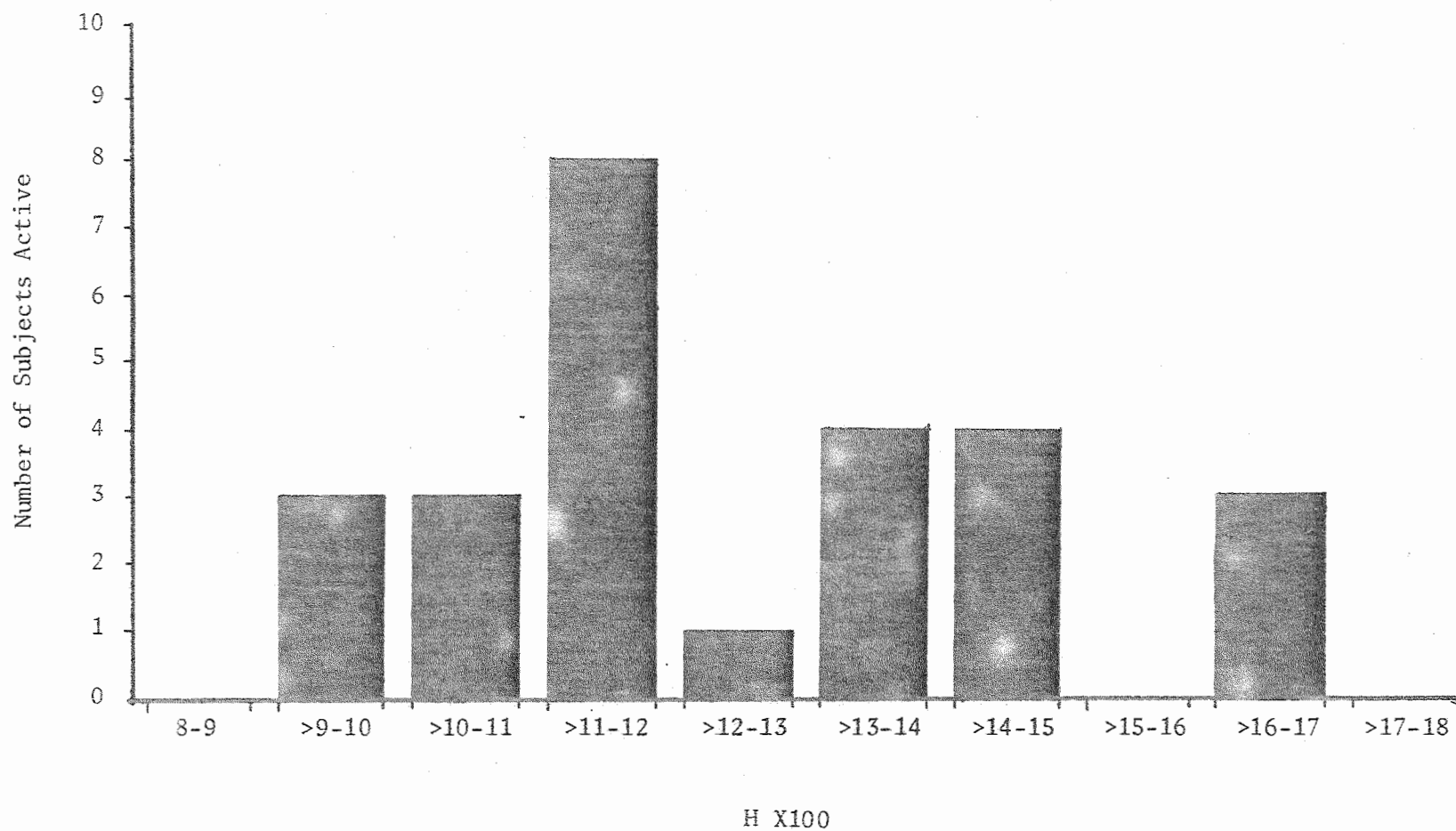
1.5.4 Diurnal Variations in General Activity

The relationship between the times of day and general activity is summarised in Fig.18. Diurnal observation-periods generally commenced at 800 h and were concluded at 1800 h. No snakes were observed during the 8-900 h, 15-1600 h and 17-1800 h periods. As Fig.18 indicates the number of animals observed to be active during the midday period, i.e. from 1100 to 1400 h, appeared to increase but frequency of captures decreased in the afternoon.

A chi-squared test applied to the data, yielded a value of 21.7 (df=9). This was significant ($P < 0.01$) and the results clearly suggest that the number of snakes at risk of being captured during the period 800-1800 hours is not constant but fluctuates considerably during that period. The twenty h devoted to crepuscular and nocturnal observations were undertaken in two h sessions distributed over non-consecutive evenings. These observations failed to yield positive results because no snakes were sighted during any of the sessions.

In summary, the results suggest that *N.a. humphreysi* becomes active (i.e. emerges from home-sites) at ca. 900 hours. More animals emerge as the day continues, and a decrease in the numbers of active individuals occurs at the onset of the evening.

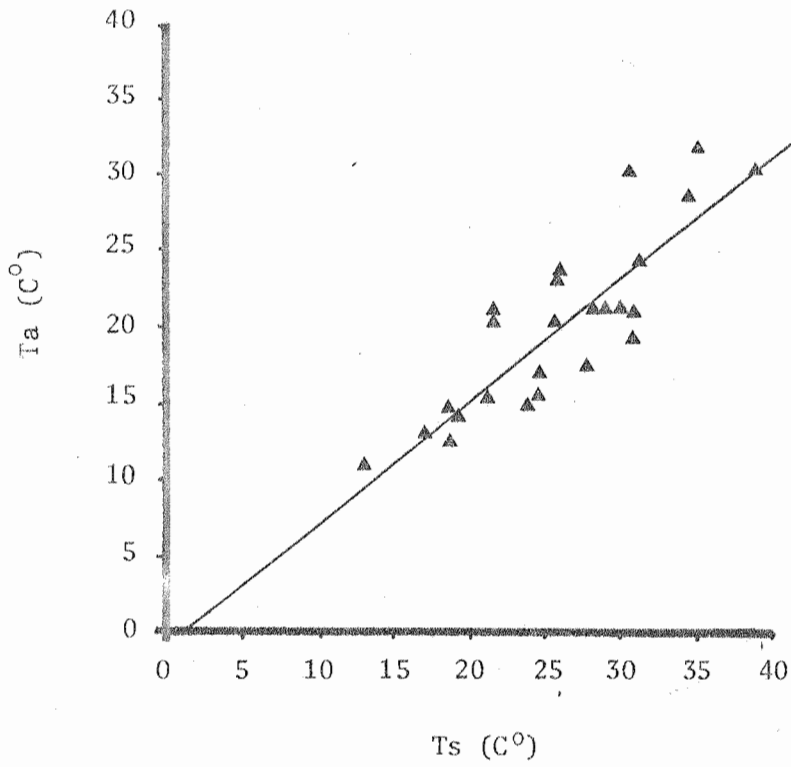
FIG.18 NUMBER OF SUBJECTS OBSERVED ACTIVE DURING DAILY OBSERVATION PERIODS, IN RELATION TO TIME OF DAY.



1.5.5 The Relationship of Ambient Temperature (T_a) to Substrate Temperature (T_s)

The data presented in Fig.19 indicate that a simple linear relationship exists between ambient-temperatures and substrate-temperatures in all of the habitat-types investigated ($r=0.8$). As may be expected, substrate-temperatures increased with increasing ambient-temperatures. The relevant data are shown in Table 2.

FIG. 19 THE RELATIONSHIP OF AMBIENT TEMPERATURES TO SUBSTRATE TEMPERATURES IN THE STUDY AREA.

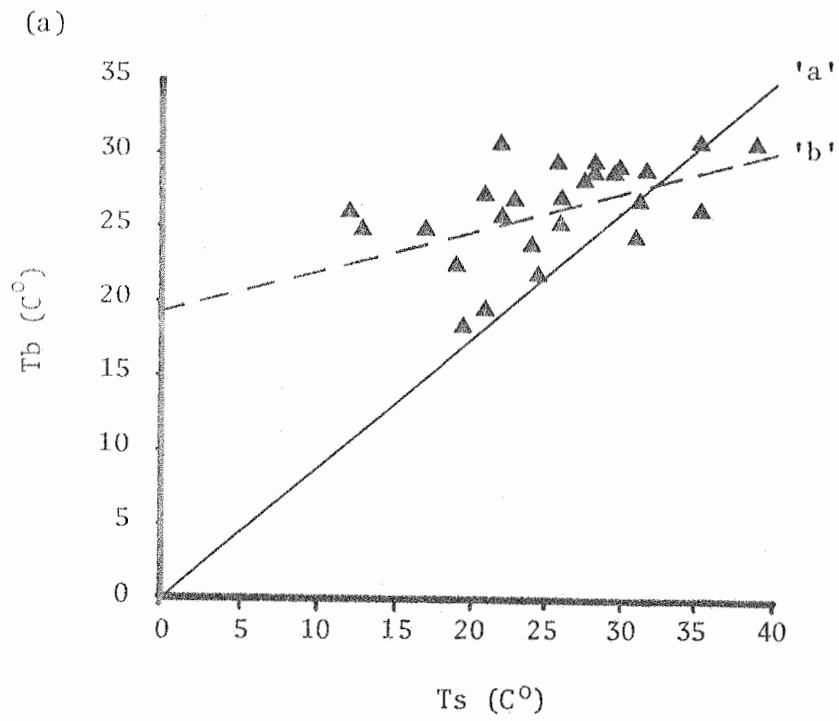


1.5.6 Relationship of Body Temperatures (Tb), Ambient Temperatures (Ta) and Substrate Temperatures (Ts)

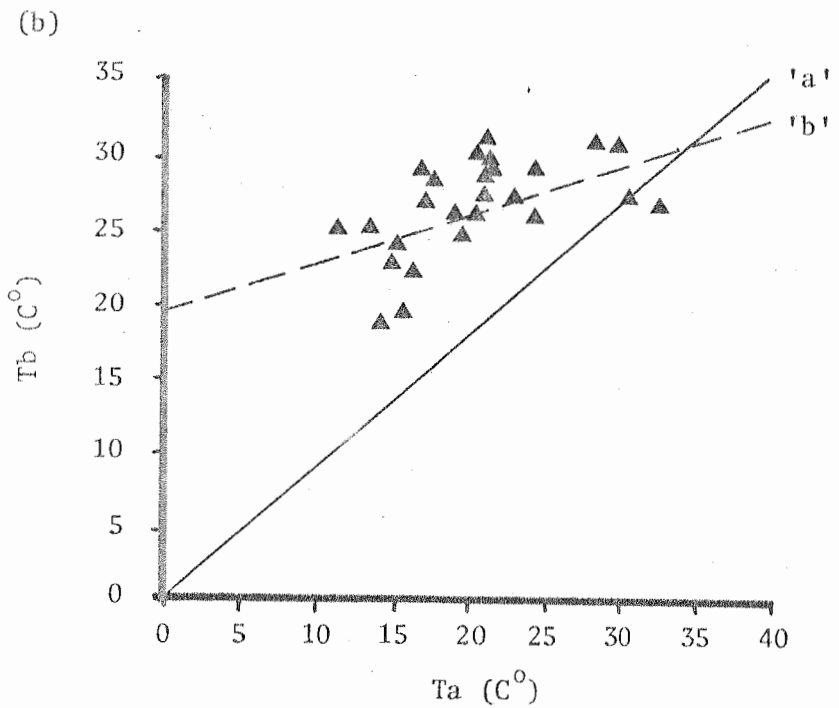
A comparison of the data illustrated in Fig.20a and 20b indicates that body-temperatures are more closely related to substrate-temperatures than to ambient-temperatures, as recorded values of body-temperatures were more evenly dispersed around the regression line of a direct correlation relationship (i.e., where Y is equal to X at any given point). Fig.20a shows that body-temperatures generally tended to be higher than ambient-temperatures, distributed above the regression line 'a'.

The slope of regression line 'b' illustrated in Figs.20a and 20b indicates that body-temperatures increase as both ambient and substrate-temperatures rise ($r = 0.55$ and 0.53 , respectively). Mean body-temperatures were 26.5°C , mean ambient-temperatures 20.2°C and mean substrate-temperatures 25.9°C . This further suggests that body-temperatures are more closely related to those of the substrate than to ambient temperatures. All of the data used in detailed analysis were based on quantitative records listed in Table 2.

FIG. 20 BODY-TEMPERATURES OF SUBJECTS IN RELATION TO ENVIRONMENTAL TEMPERATURES IN THE STUDY-AREA.



a) Substrate-temperatures.



b) Ambient-temperatures.

1.5.7 Sex-related Differences in Temperature

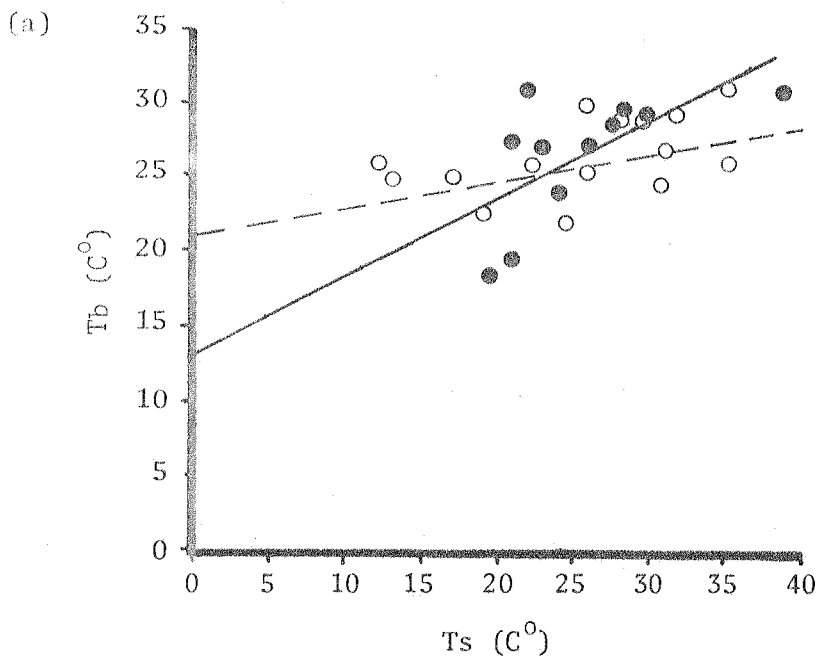
Data selected from Table 2 are shown in Figs. 21a and 21b to demonstrate sex-related differences and relationships of temperatures, based on the relations of body-temperatures-substrate-temperatures, and body-temperatures-ambient-temperatures, respectively. Paired regression analyses clearly indicate that the body-temperatures of male subjects were more closely correlated with both substrate and ambient-temperatures ($r = 0.50$ and 0.70 , respectively) than those of females. Corresponding values obtained for female subjects were 0.50 for both pairs of correlations. The differences appeared to be associated with the maintenance of higher body-temperatures by females than by males at lower ambient- and substrate-temperatures.

The mean value of body-temperatures obtained for female subjects was 26.60°C and that estimated for males was 26.55°C , whereas the mean ambient-temperature experienced by females was 20.53°C , that experienced by male subjects was 19.64°C . Corresponding mean substrate-temperatures were 24.10°C and 26.68°C . The results indicate that the mean values of body-temperatures recorded for males and females were very similar (within 0.05°C) and that the mean values obtained for both sexes are closer to the mean substrate-temperatures than to mean ambient-temperatures.

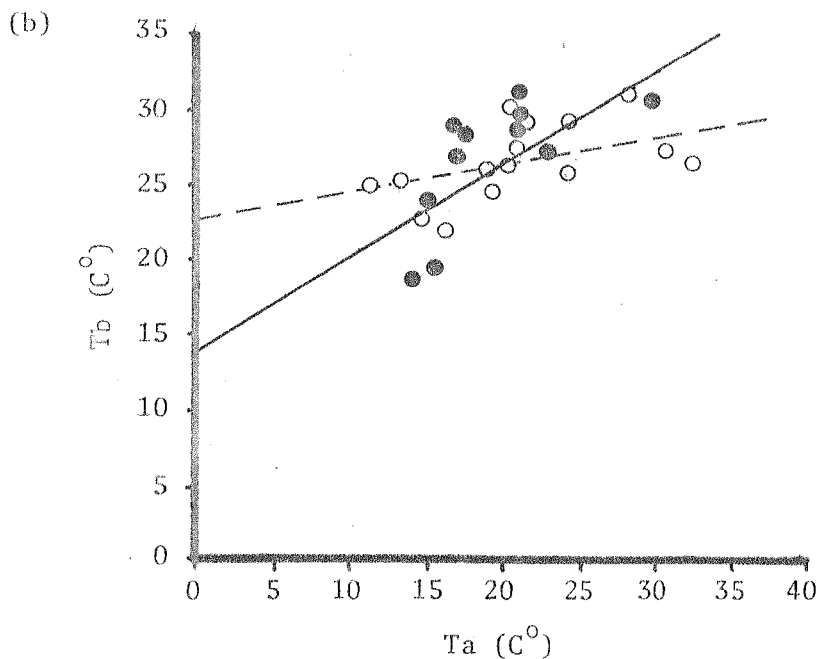
FIG. 21

SEX-RELATED BODY-TEMPERATURES OF SUBJECTS IN RELATION TO ENVIRONMENTAL TEMPERATURES.

Solid symbols and continuous regression line relate to males, open symbols and interrupted regression line to females.



a) Substrate-temperatures.



b) Ambient-temperatures.

1.5.8 Relationships of Temperature to Body-length

In attempting to determine whether any relationship exists between body-temperatures and the length of individual snakes, it was considered essential to establish *ab initio*, whether records of subjects of different lengths were significantly biased with respect to substrate and/or ambient-temperatures. The data presented in Fig. 22a and 22b illustrates the relationship between the lengths of the snakes examined and the corresponding environmental temperatures recorded. Although the subjects appeared to be randomly distributed with respect to lengths and temperature-ranges, regression analysis disclosed a slight bias favouring the longer snakes. These were more often recorded at higher substrate- and ambient-temperatures. Correlation coefficients, yielded the values, $r = 0.06$ and $r = 0.09$ respectively.

Fig.23a is based on body-temperatures of subjects in relation to individual length established for 26 subjects examined in natural conditions. Regression analysis of these data indicates that as body-lengths increase, body-temperatures decreased ($r = 0.17$). The results suggest that if any relationship exists between body-temperatures and body-length at all, it is limited to a slight tendency for longer animals to have lower temperatures than smaller individuals, although longer snakes were generally captured at higher environmental temperatures.

FIG. 22 INDIVIDUAL LENGTHS OF SUBJECTS IN RELATION TO ENVIRONMENTAL TEMPERATURES.

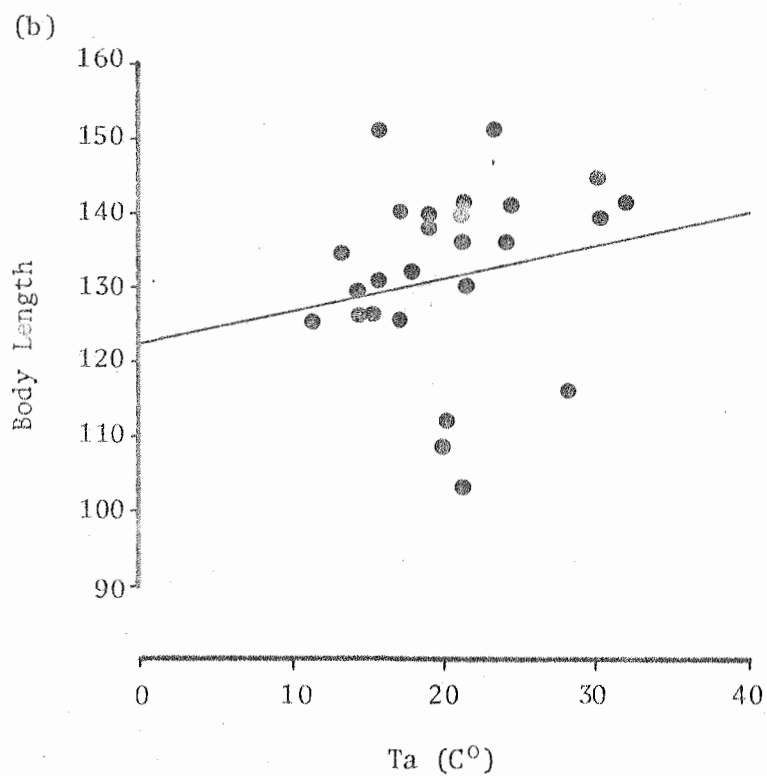
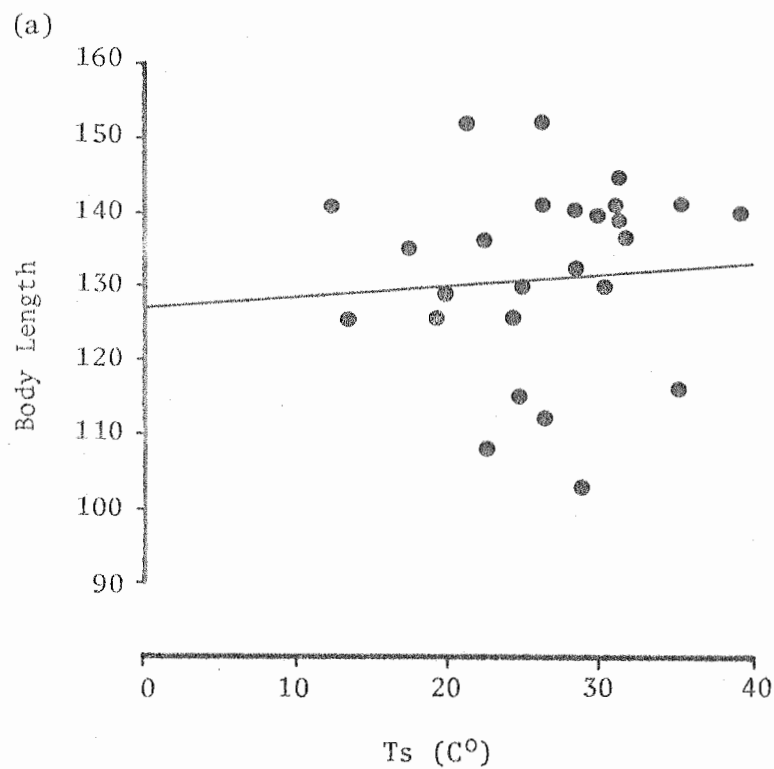
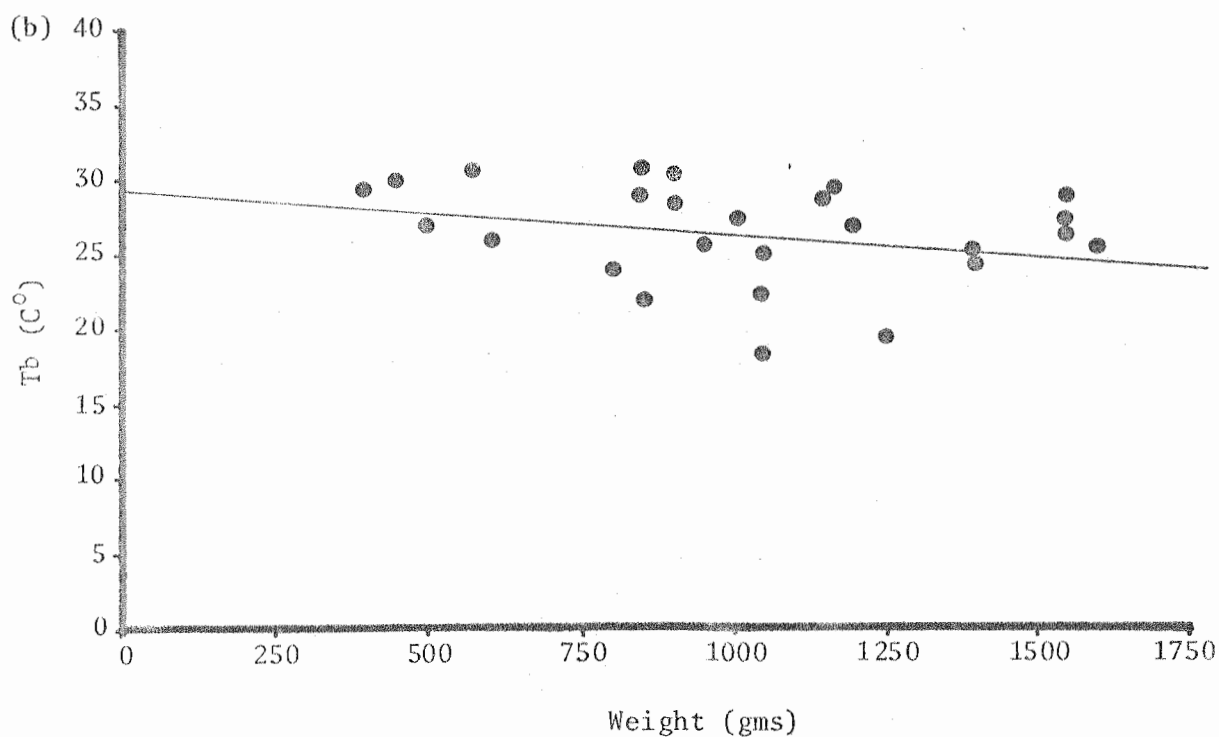
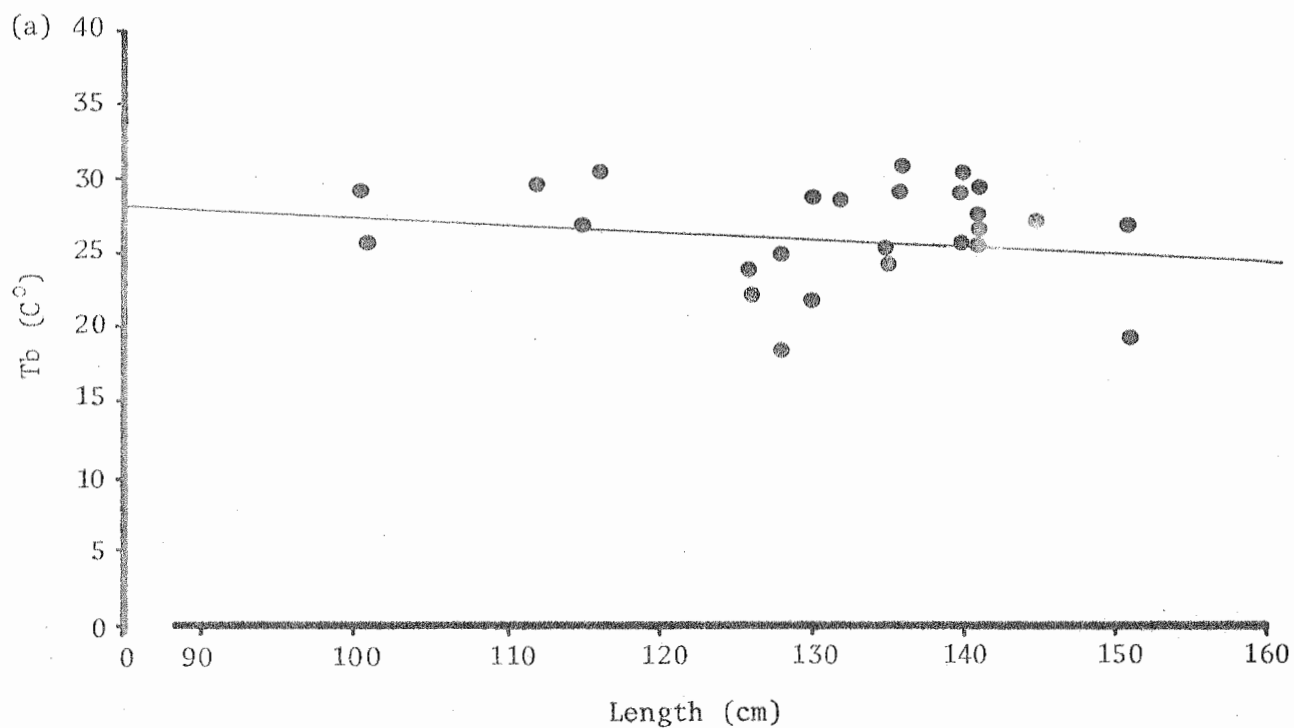


FIG. 23 BODY-TEMPERATURES OF INDIVIDUAL SUBJECTS IN RELATION TO LENGTH AND WEIGHT.

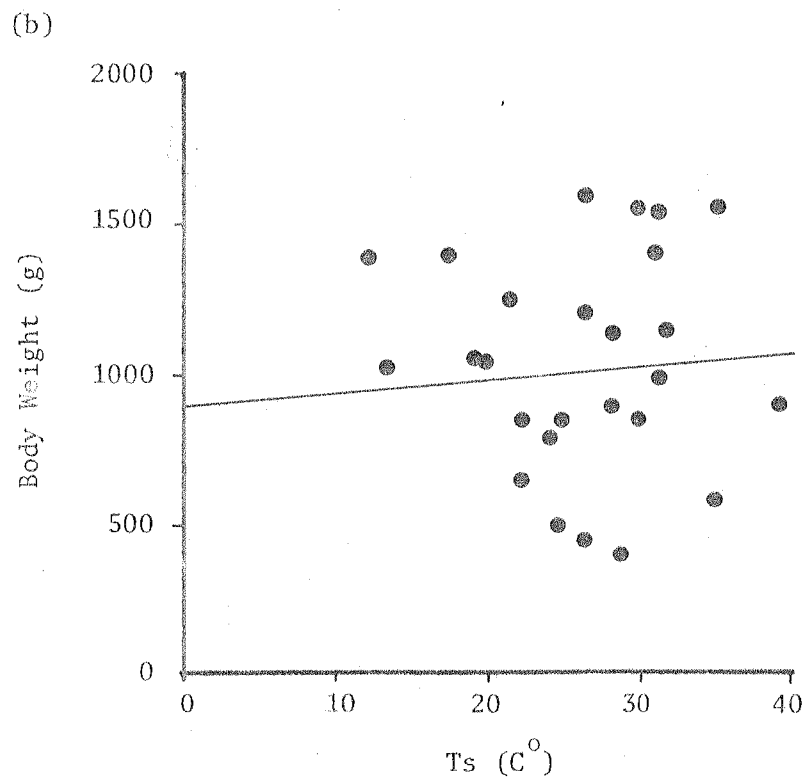
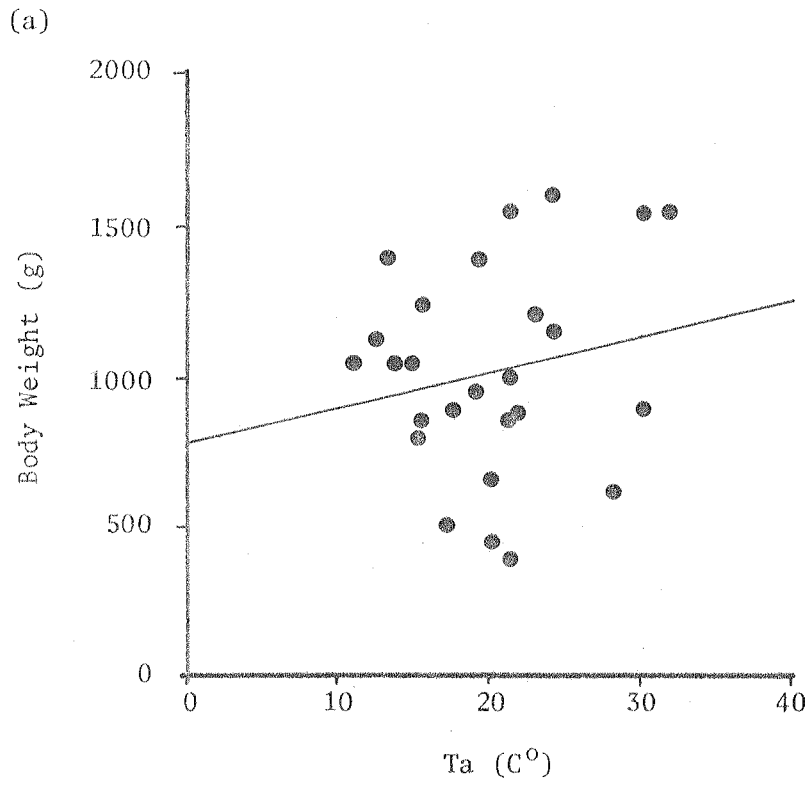


1.5.9 Relationships of Temperatures to Body-weight

The data relevant to assessing the relationships between temperature and the body-weights of individuals were analysed by the same methods employed in examining variables in Section 1.5.8. The results are graphically summarised in Figs.24a and 24b, illustrating the relationships of body-weight to substrate- and ambient-temperatures. When these results are compared with those relating to temperatures and body-length, they appear to exhibit somewhat parallel trends, in that subjects of greater weight were recorded at slightly higher substrate- and ambient-temperatures, as were longer individuals. The correlation coefficients calculated for the relationships of body-weight and substrate- and ambient-temperatures were, $r = 0.06$ and 0.05 respectively.

Fig.23b, based on the relationship of body temperatures to body-weight demonstrated that body-temperatures decreased slightly with increasing body-weight. The value of the correlation coefficient obtained for this relationship was $r = -0.28$.

FIG.24 INDIVIDUAL WEIGHTS OF SUBJECTS IN RELATION TO ENVIRONMENTAL TEMPERATURES.



1.5.10 Relationships of Temperature to Activity-status

Of the 26 animals examined in the field, seventeen were actively foraging and nine were basking when captured. A comparative summary of the temperatures recorded in conjunction with each category based on activity-status is presented in Table 6. The mean body-temperature of 27.53°C obtained for foragers and that of 24.66°C for subjects engaged in basking represents a difference of 2.87°C between the categories. Compared with an expected mean of 26.10°C , the calculated chi-squared value (0.16) showed that there was no significant variation ($.70 > p > 0.50$), because the critical value ($p = 0.05$) would have required a chi-squared value of 3.84.

The mean ambient temperatures of 21.18°C obtained for foragers and 18.22°C obtained for basking animals indicate a difference between the sexes amounting to 2.96°C whereas corresponding substrate-temperatures differed by 2.94°C . In all recorded instances the mean basking-temperatures were lower than foraging-temperatures. Ranges, standard deviations and standard errors of the calculated values are also given in Table 6.

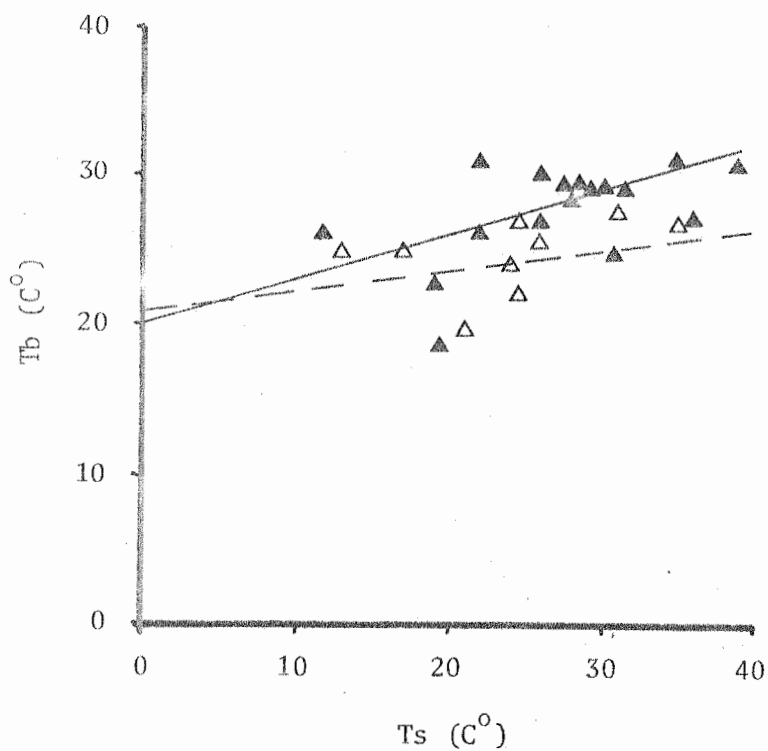
Fig.25 shows the relationship of body temperature to substrate temperature in basking and foraging subjects. The data and regression-lines illustrated provide some indication that foraging individuals tend to maintain higher body-temperatures than basking conspecifics. The correlation coefficients obtained for foragers and for baskers were $r = 0.50$ and $r = 0.40$ respectively.

TABLE 6 : TEMPERATURE DATA IN RELATION TO ACTIVITY-STATUS.

Subjects Foraging (N=17)			Subjects Basking (N=9)		
Tb	Ta	Ts	Tb	Ta	Ts
18.5	14.0	19.5	19.5	15.5	21.0
22.5	14.5	19.0	24.0	15.0	24.0
29.5	21.0	28.5	22.0	15.5	24.5
28.5	17.5	28.0	27.0	17.0	24.5
24.5	19.0	31.0	27.5	21.0	31.0
29.0	21.0	29.5	26.5	32.0	35.0
29.0	24.0	31.5	25.0	13.0	17.0
27.0	23.0	26.0	25.0	11.0	13.0
31.0	28.0	35.0	25.5	24.0	26.0
30.5	30.0	39.0			
27.0	30.0	31.0	\bar{X} = 24.66	18.22	24.00
26.0	19.0	12.0	Range = 8.0	21.0	22.0
29.0	21.0	30.0	SD = 2.55	6.49	6.65
29.0	17.0	28.0	SE = 0.35	2.16	2.22
30.0	20.0	26.0			
31.0	21.0	22.0			
26.0	20.0	22.0			
\bar{X} = 27.53	21.18	26.94			
Range = 12.5	16.0	27.0			
SD = 3.30	4.70	1.14			
SE = 0.30	1.14	1.58			

FIG. 25 BODY TEMPERATURES OF SUBJECTS OF DIFFERENT ACTIVITY-STATUS IN RELATION TO ENVIRONMENTAL TEMPERATURES.

Closed symbols and continuous regression line relate to foraging, open symbols and interrupted regression line to basking animals.



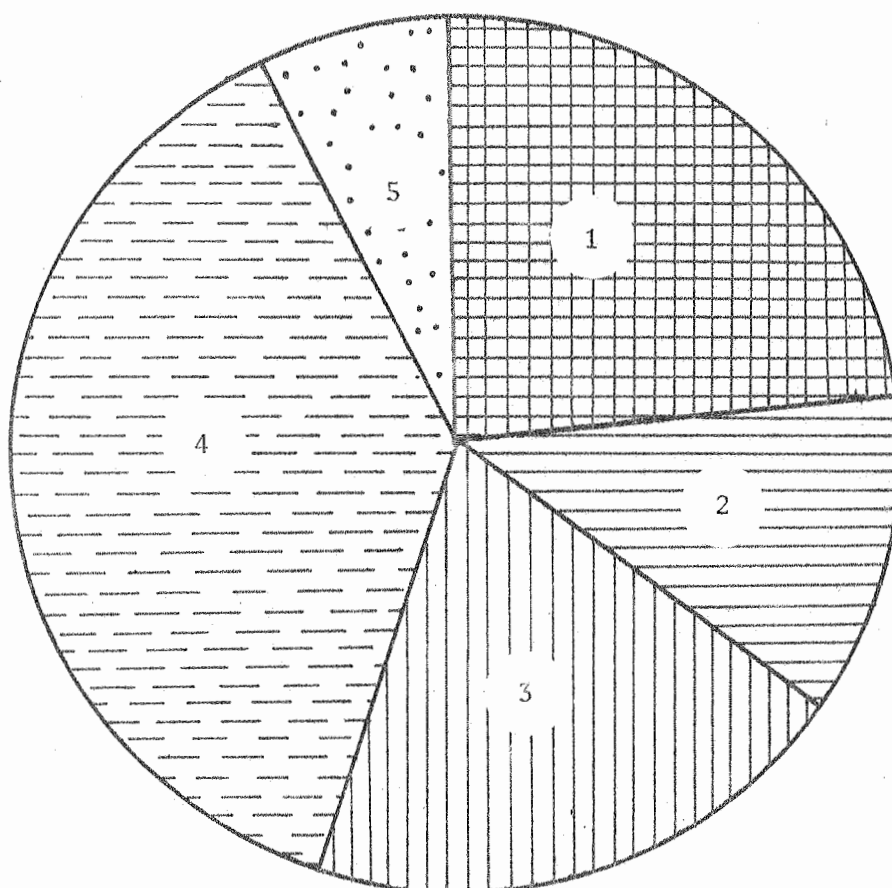
1.5.11 Habitat Utilization

Analysis of data related to habitat-utilization based on quantitative values included in Table 2, is further shown in Fig.26. The number and relative proportions (percentages) of subjects in each habitat-type calculated from records obtained for 26 individuals is as follows:

<u>Habitat Type</u>	<u>Number of Individuals</u>	<u>Relative Proportion of Individuals %</u>
1	6	23.08
2	3	11.50
3	5	19.22
4	10	38.50
5	2	7.70

The results indicate differential utilization of habitats ranked in the order of types four, one, three, two and five. These results may be compared to the distribution of subjects based on direct sightings, shown in Fig.3. A more detailed description of various habitat-types is provided in Section 1.4.1(k).

FIG.26 RELATIVE PROPORTIONS (PER CENT) OF VARIOUS HABITAT-TYPES UTILIZED BY *N.A. HUMPHREYST.*



HABITAT TYPES

1. Rock outcrops
2. Fallen timber
3. Open grassland
4. Small rock outcrops occurring with grassland
5. Dense vegetation

1.5.12 Site-specific Differences in Biomass

During the period of compiling records and observational exercises in natural conditions it became evident that the population of *N.a. humphreysi* at Brownwater Lagoon had a different, considerably higher biomass than that of the Silverwater Plains study-site. The data obtained for each of these sites are shown in Table 7. As the estimated values indicate the total biomass (measured in g.) at Site 1 was almost twice that of Site 2; as was the mean body weight of subjects. However, the mean lengths of snakes examined at Site 1 was only fifteen cm more than those recorded at Site 2; in the former locality snakes tended to be more robust than in the latter area.

The relationship between the weights and lengths of subjects recorded at each site is shown in Fig.27. Although the regression line plotted for subjects obtained from Site 1 falls closer to a direct linear relationship, (where Y is equal to X at any given value) than that plotted for animals from Site 2, the correlation coefficient estimated for those of Site 1 was 0.3, compared to 0.9 for those of Site 2. This suggests that the subjects occurring at Site 2 were characterised by a weight-length relationship that was more strictly linear than that obtained for individuals at Site 1. However, animals at Site 1 showed a higher level of correlation in terms of correspondence of weights and lengths than subjects at Site 2, which yielded estimated values of body weights that were generally lower in relation to their individual lengths.

TABLE 7 : BODY-LENGTHS, WEIGHTS AND SEX OF SUBJECTS IN THE STUDY-AREA.

Site I : Brownwater Lagoon

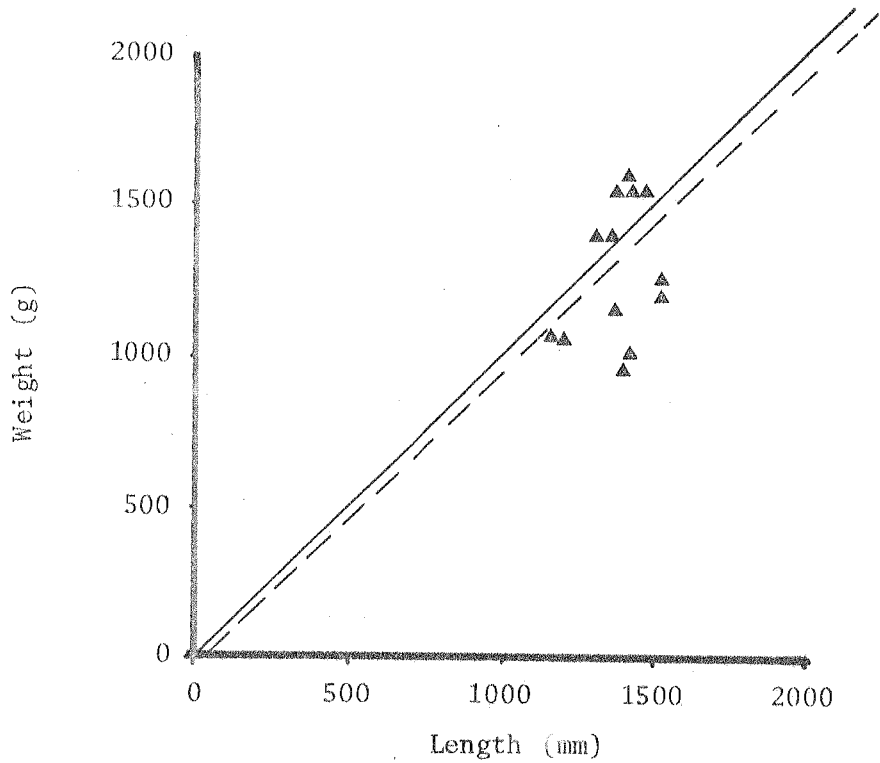
S no.	Length	Weight	Sex
1	151 cm	1250 g	M
2	129	1050	M
3	126	1050	F
9	141	1000	M
10	138	1400	F
11	140	1550	F
12	136	1150	F
13	151	1200	M
16	141	1550	F
17	145	1550	F
18	140	950	F
20	135	1400	F
26	141	1600	F
Total biomass = 16700 g			
\bar{X} weight = 1284.6 g			
\bar{X} length = 139 cm			
N = 13			
Sex-ratio = 9F : 4M			

Site II : Silver Plains Creek

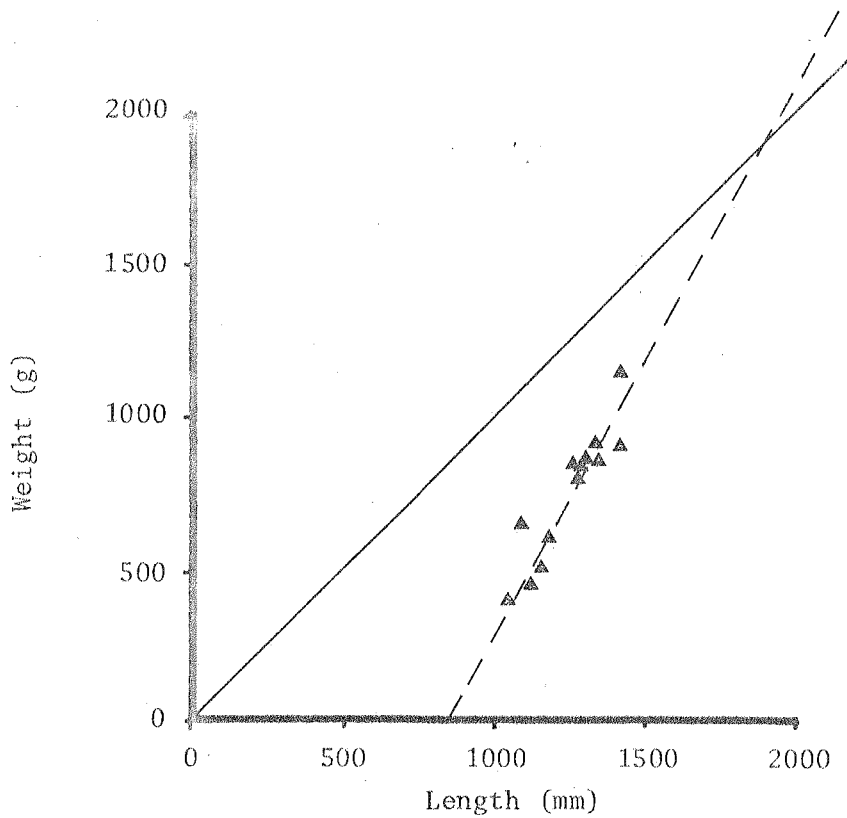
S no.	Length	Weight	Sex
4	126 cm	800 g	M
5	130	850	F
6	115	500	M
7	103	400	M
8	132	900	M
14	116	600	F
15	140	900	M
19	130	850	M
21	125	850	F
22	140	1150	F
23	112	450	F
24	136	850	M
25	108	650	F
Total biomass = 9750 g			
\bar{X} weight = 750 g			
\bar{X} length = 124 cm			
N = 13			
Sex-ratio = 6F : 7M			

FIG.27

RELATIONSHIPS OF INDIVIDUAL BODY-WEIGHTS TO BODY-LENGTH OF SUBJECTS IN THE PRINCIPAL STUDY AREAS. The continuous regression-line relates to a direct correlation; the interrupted regression line is applied to actual data obtained in the field.



(a) Brownwater Lagoon



(b) Silver Plains Creek

1.6 DISCUSSION

1.6.1 Home-sites and Habitat Utilization

The regular utilization of permanent home-sites evident throughout the study area (see Section 1.5.1) suggests a consistent adaptation to a limited number of available habitats. In situations where both rock and timber shelter were available as possible home-sites, the rock-outcrops were invariably selectively utilised. The short trail, post-emergence basking pad, and the pre-foraging basking pad were the most prominent features, and these were characteristic of the majority of home-sites that were examined. It is not known whether such features are unique to home-sites of *N.a. humphreysi*, because comparable phenomena have not been previously described in other large elapid snakes. However, it appears improbable that such characteristics are confined exclusively to *N.a. humphreysi*, as this species inhabits similar general habitats to those of *N.s. scutatus* and other species of elapids of continental Australia. This is further discussed below. It is possible that the apparent lack of documented evidence relating to characteristics of home-sites is a consequence of inadvertent neglect of this aspect of the biology of snakes by previous investigators. However, it is possible that other species of elapid snakes are more mobile, consequently they may not maintain a permanent home-site comparable to that described in the present study.

As discussed in Section 1.5.11, a higher proportion (percentage) of the 26 subjects that were examined in the field were found to utilise habitat type four (rock outcrops situated grassland) and a lower proportion appeared to be associated with habitat-types one, three, two and five. The results showed that sixteen of the 26 animals examined occurred in rocky habitats. Since 80% of the 50 permanent home-sites that were examined in detail were within or beneath rocks, it may be concluded that *N.a. humphreysi* has adapted to establishing regular home-sites on this type of substrate, at least in the study-areas examined in the course of the present investigation.

Shine (1977) established that *N.s. scutatus* exhibits a high level of selective adaptation to lowland-swamp habitats in the New England area, with a reduced predilection for streams and permanent

bodies of water (88%, 6% and 6%, respectively). These observations are in substantial accordance with the distribution of *N.a. humphreysi* observed in the present study. Very much larger numbers of specimens were noted to occupy the perimeter of swampy areas, for example, Brownwater Lagoon and Silverplains Creek, which are bordered by swamps and fewer snakes were recorded on higher, or more densely forested terrain.

On the basis of the present investigation, it can be established that *N.a. humphreysi* occupies habitats similar in essential characteristics to those occupied by *N.s. scutatus* on the Australian continent. Other species of elapids examined by Shine (1977), specifically *A. superbus*, *P. porphyriacus* and *P. textilis* were not recorded as inhabitants of lowland swamps but the same species were found in highland swamp, stream and dry habitats, respectively. Shine's classification of the above habitat types incorporates the lowland swamps into a 800 m to 1300 m elevation class. Under this classification, the Lake Sorell - Lake Crescent area can also be categorized as being lowland swamp type habitat, consequently *N.a. humphreysi* and *N.s. scutatus* appear to occupy similar habitat-types at similar elevations.

1.6.2 Activity-ranges and Distribution

Estimates of the activity-ranges of individuals of *N.a. humphreysi* investigated in the present study were obtained from observations on single bouts of foraging activity. In all of these instances, identified subjects were observed to leave their home-sites, forage, then return to a home-site. The results of these observations showed that the snakes may move as little as four m or as far as 50 m in the course of a single foraging bout. However, foraging distances, based on movement in a single bout, differ from the distance an individual snake may travel during the course of one season. For example, subjects seven, eleven and twelve were recorded at different home-sites than those they occupied on the occasion of their initial capture. This indicates that during a single season individuals may move freely throughout the available habitat, utilizing any of a number of permanently established home-sites at different or consecutive times.

After it was released and permitted to return to its home-site, subject thirteen was recorded as captured at a distance of twenty m from the home-site it had elected to re-enter. However, this animal may have covered a considerably greater amount of territory than the twenty m measured in a direct line from capture-site to home-site. The method of radiotelemetry employed by Shine (1979) for determining the activity-ranges of *N.s. scutatus* (see Section 1.4.1) would be most useful in determining similar parameters in *N.a. humphreysi*. However, in the present study, the activity-range would probably be of a more linear shape than that found in *N.s. scutatus*, since the snakes investigated here occupied home-sites around the perimeter of a lagoon and the bed of the creek. The unavailability of documented data relating to individual activity-bouts such as those investigated in the present study does not permit direct comparison of *N.a. humphreysi* with other species. However, it appears that the activity-range of this species may be comparable to that of *N.s. scutatus*, if similar techniques of assessing activity-range were employed.

The distribution of *N.a. humphreysi* within the Lake Sorell - Lake Crescent study area appears to be related to three major categories of environmental factors. The first (and perhaps the most obvious) of these is the availability of potential home-sites within the area, the second is the geographical aspect of prospective home-sites (in relation to exposure to radiation) and the third is the availability and abundance of food. Aspects of food-resources, prey-species and their utilization are discussed in Section 2.4.

Study sites I and II differed markedly in terms of the availability of home-sites. The most notable difference was related to the distribution of rock-piles; these occurred at regularly-spaced intervals along the banks of Silverplains Creek, whereas they occurred as clumps around the perimeter of Brownwater Lagoon. A comparison of the positions of prominent rock-outcrops (Fig. 7) and the recorded distribution of snakes (Fig. 13) clearly illustrates the close association of the animals with rocky terrain. The clumped distribution-pattern of the subjects recorded at Brownwater Lagoon is presumably due to their preferential utilization of home-sites as much as, or more than any other environmental factor. The more regularly-distributed pattern of occurrence of individuals evi-

dent at Silverplains Creek (Fig. 14) is probably a consequence of the regular distribution of rock-outcrops present at that study-site.

When considering the aspect of the home-sites present at each study-site, it is important to note that in both of the areas investigated, the communities of vegetation were considerably more dense at the northern borders of the sites, than at their southern border. This resulted in an increased exposure of the home-site at the southern perimeter to direct radiation and consequently slightly drier and warmer conditions than those prevailing at the home-sites at the northern perimeter.

As Fig. 13 illustrates, the spatial distribution of *N.a. humphreysi* was more dense on the rock-outcrops at the southern perimeter of Brownwater Lagoon than in other areas around the lagoon. It appears that, although the surface of the southern outcrop is no larger than those of the western and eastern outcrops, the aspect of the home-sites, or the general aspect of the habitat, results in larger numbers of animals inhabiting this area. However, the distribution of snakes at Silverplains Creek appears to be more closely related to the availability of specific habitats; i.e. regularly distributed rock-outcrops, than to aspect. The majority of snakes recorded in this area were either captured in the dry bed of the creek or on the northern perimeter of the creek.

The density of the vegetation along the southern perimeter at Silverplains Creek was relatively low, consequently grazing-pressure (by cattle and sheep) was high in comparison with the more densely-vegetated areas. A similar situation occurred along the eastern perimeter of the Brownwater Lagoon study-site. Therefore, although the sparsely-vegetated habitats were dry and warm, the presence and activities of sheep and cattle may have prevented inhabitation by snakes. This was clearly shown in the Brownwater Lagoon area where, although suitable rock outcrops occur on the eastern perimeter of the lagoon, the sparseness of the vegetation permits high grazing pressure to develop and this probably precluded the establishment of permanent home-sites by snakes.

Following an investigation of the effect of vegetation-density on the activity of several species of ribbon snake (*Thamnophis* sp.),

Tinkle (1957) stated that "early in the year the ribbon snakes utilized the open areas of the main ridge where they obtained maximum exposure to sunlight. As temperatures rose during the later months, the snakes moved into shaded areas to avoid excessive heat. Therefore, under one set of conditions shading of the habitat produced one effect and under another set, the opposite effect on animals". Fitch (1949) reported similar observations on a population of rattle snakes (*Crotalus viridis*). This pattern of shade-related migration was not observed in the present study of *N.a. humphreysi*, at least during the three months of the observation period. In fact, subjects appeared to be restricted in their movements by the availability of home-sites, density of vegetation, regular exposure to adequate radiation, or by the presence and/or abundance of prey-species within the microhabitats that were examined. Shuttling from shade to sun may have been accomplished on a much smaller scale in *N.a. humphreysi* than is the ribbon snakes and rattle snakes. The potential importance of these factors may support the postulation that the study sites which were investigated were "island-type" habitats, as far as the activities of the snakes were concerned, because of physical restrictions on migration imposed by environmental factors operating within the area.

1.6.3 Diurnal Variation in General Activity

The fact that individuals of *N.a. humphreysi* were observed to be active mainly around the middle of the day, in the Lake Sorell - Lake Crescent study-area may be a reflection of the characteristic temperature-regime associated with the central plateau region. Since these animals, as all poikilothermous terrestrial vertebrates, rely on environmental temperatures to maintain optimal body-temperatures, a direct relationship may be expected to occur between activity-levels and environmental temperatures. The mean maximum temperature at the study-site was 16.5°C and the mean minimum was 3.8°C; however, the mean maximum temperature in the warm season, when the snakes are most active, was 19.68°C. Since the mean minimum monthly temperatures (recorded at night) were considerably lower than the mean maximum temperatures, it is reasonable to assume that the gradual warming of the substrate, following sunrise, requires a prolonged period of time. This is probably reflected in the fre-

quencies of active snakes, with more animals becoming conspicuous by their presence as the day warms and the numbers declining as the day cools (Fig. 18). Actual body-temperatures of the snakes are discussed in later sections.

Shine (1979) suggested that large representatives of the colubrids, crotalines and viperids may usually be nocturnal or crepuscular, possibly because these are the times when their major prey-species (small mammals) are most abundant or active. However, since the most common prey-species utilized by the majority of large Australian elapids are reptiles or amphibians, most of the Australian elapids are diurnal. Shine (*op cit.*) also found that *A. superbis* was active between 0900 and 1600 h, *N.s. scutatus* from 0800 to 1700 h, and *P. porphyriacus* from 0800 to 1700 h. These observations correspond well with those made on *N.a. humphreysi* in the course of the present study; the subjects of this were active from 0900 to 1700 h. The results are also consistent with data collected by Worrell (1963), Rawlinson (1965) and Cogger (1975) in studies of Australian elapids, and by Gibson and Falls (1979) in an investigation of North American colubrids.

1.6.4 The Effect of Cloud-cover on General Activities and Body-temperatures.

The results presented in Section 1.5.3 and illustrated in Fig. 15 clearly indicate that the influence of cloud-cover on the activity of *N.a. humphreysi* is minimal. This suggests that as thigmothermous animals these snakes rely more closely on substrate-temperatures for thermoregulation than on direct radiation obtained by exposure to the sun. Consequently, the snakes become active on completely overcast days as well as on clear, cloudless days, provided that the substrate temperatures are sufficiently high to permit activity.

The effect of cloud-cover on the body-temperatures of the animals is also minimal. As may be expected, for animals with body-temperatures closely related to environmental temperatures, body-temperatures decline slightly as direct radiation is reduced by the presence of clouds (Fig. 17). Although the body-temperatures were

observed to decrease, optimal, or mean preferred, body temperatures must have been maintained successfully throughout the range of recorded cloud-cover percentages. This is evidenced by the fact that activity of the snakes was sustained regardless of the extent of the cloud-cover. Gibson and Falls (1979) were able to show that the body-temperatures of the common garter snake (*Thamnophis sirtalis*) decreased as cloud-cover increased. Their observations indicated that in conditions associated with clear sunny skies, the body temperatures of subjects were maintained at a mean value of 1.7°C higher than those recorded for *N.a. humphreysi*. Under cloudy conditions, specimens of *T. sirtalis* maintained a mean body-temperature 4.05°C higher than the snakes observed in the present study. By comparison, it would appear that *N.a. humphreysi* has a greater range of tolerance to fluctuations of environmental temperatures than does *T. sirtalis*.

Inasmuch as *N.a. humphreysi* is a cold-climate elapid, and therefore likely to experience a relatively high percentage of cloudy days in the course of any given activity season, it seems reasonable to assume that a greater tolerance to low temperature associated with increased cloud-cover would occur in this species. The main ecological adaptive advantage of this tolerance is presumably that foraging activity could continue regardless of the fluctuations of cloud-cover, as long as substrate-temperatures provided adequate conductive heat to permit the animal to maintain an optimal or preferred body-temperature.

1.6.5 Relationships of Body-temperatures (Tb) to Environmental Temperatures (Ts and Ta).

Having established that a direct relationship occurs between ambient temperatures (Ta) and substrate temperatures (Ts), in Section 1.5.5, it is possible to compare the relationship between these environmental temperatures and the body-temperature of individual subjects of *N.a. humphreysi*. As may be expected from a thigmothermic reptile, there was a much closer relationship between Tb and Ts than between Tb and Ta. The fact that the mean Tb differs from the mean Ts only by 0.6°C compared to a deficit of 6.3°C between mean Tb and Ta, clearly indicates the relatively close association between the

former variables. Similar results, both in terms of correlation coefficients and comparison of means, were obtained by Gibson and Falls (1979). However, there is a conspicuous general absence of documented data on the relationships of T_s , T_a and T_b , in large elapid snakes and therefore direct comparisons are not possible.

1.6.6 Relationships of Temperature to Activity-status.

It is evident from the data presented in Table 6 that the mean body-temperatures recorded in foraging subjects was higher (by 2.87°C) than those recorded in basking animals. This difference was probably a result of the higher levels of metabolism associated with active foraging, requiring a higher temperature and as a consequence, a greater range within which cooling can take place. However, it should be noted that, in the present study, the substrate temperatures recorded while observing foraging subjects yielded a mean value 2.94°C higher than those recorded for basking animals. This appears to indicate that the maintenance of a preferred body-temperature is mainly dependent on the current substrate-temperature and that a mean value of almost 3°C constitutes the difference between a preferred foraging body-temperature and the basking body-temperature. The basking temperature in this case is not necessarily a preferred temperature but is most likely to be the "warming" temperature (associated with the warming phase of the initial process of post-emergence thermoregulation).

Since the lowest body temperature recorded in a foraging individual was 18.5°C and the highest recorded in a basking individual was 27.5°C , it is evident that a considerable amount of overlap occurs in terms of optimal foraging temperatures. Possible explanations for this may be that, on an individual basis, the preferred temperature of a given species depends on its internal state, and may be reduced by injury, parasitism and shedding of the skin (Kitchell, 1969). In some viviparous forms, females maintain higher body-temperatures than males, a phenomenon probably related to development of the embryos carried by the female (Stewart, 1965). In addition to these modifying factors, the individual size of the snakes or the strength of their feeding drive may be associated with

variability of the preferred foraging temperatures. Furthermore, the fact that *N.a. humphreysi* is a cold-climate elapid of large size, may enable it to become adapted to activity in cold conditions, as well as the conditions generally considered to be optimal for other, related species.

In support of the above postulation, it may be noted that Spellerberg (1972) and Heatwole (1976) recorded (in the field) mean preferred foraging body-temperatures of 20.8 C and 29.8 C, respectively, in *N.s. scutatus*. In these studies, Spellerberg was engaged in an investigation of the southern Victorian population, whereas Heatwole examined the northern New South Wales population of the species. The results clearly show that even within a single species, the preferred temperature may be altered in order to facilitate activity under different climatic regimen at different latitudes. It therefore appears reasonable to assume that a population such as that of *N.a. humphreysi* that has been isolated on a relatively cold, temperate island for some 10,000 years, has adapted its thermoregulatory processes and became more versatile with respect to its preferred foraging temperatures. This may have enabled the species to survive by being able to forage for food in cold conditions, as well as in comparatively warm conditions.

Based on results of investigations of the ecological importance of the striped and melanic phases of *T. sirtalis*, Gibson and Falls (1979) stated that "body temperatures of snakes in the field reveal that during the cooler part of the active season, melanics are able to stay warmer than striped snakes by an amount of 1.5°C. Thus, melanics have an improved ability to convert the sun's radiation to body heat, and appear to express this ability at that time of the year when maintaining an elevated body temperature presumably is most challenging". In the light of this, the melanic colouration which is most common in populations of *N.a. humphreysi*, is probably an important factor in the ability of this species to adapt to the relatively cold climate of Tasmania.

1.6.7 Sex-related Differences in Temperature.

The significance of sex-related differences in the temperature-preferenda of snakes is poorly documented, the most recent and per-

haps most extensive study being that undertaken by Gibson and Falls (1979). As a result of their investigation of *T. sirtalis*, they were able to identify several salient factors relating to sexual differences. Firstly, they determined that the body temperatures of males were 0.1°C lower than those of females during the last three months of summer; secondly, that in males frequency distributions of body-temperatures and environmental temperatures were nearly symmetrical, whereas those of females were strongly skewed to the left; and thirdly, that ambient and substrate temperatures were somewhat better predictors of body-temperature in males than in females.

In the present study, little difference was discerned to exist between the mean body temperatures of male and female subjects; the difference was only 0.05°C and females had higher mean body-temperatures. Although the difference was negligible, the results nevertheless agree with those obtained by Gibson and Falls (1979), suggesting that females of terrestrial snakes may generally have higher body-temperatures, than males of the same species. Figs. 21a and 21b illustrate that the relationship of body temperatures to environmental temperatures recorded in *N.a. humphreysi* are similar to those of *T. sirtalis*. The fact that the females of both species have frequency distributions skewed to the left indicates that both may be clustered closer to the upper thermal limits than the males.

The results of the present investigations, similarly to those of Gibson and Falls (*op cit.*), indicate that both ambient and substrate temperatures were more directly related to the body temperatures of male subjects than to those of females. Although a direct comparison between species of a North American colubrid and a southern Australian elapid may not be feasible, the observations described above suggest that females of both species appear to be able to thermoregulate more precisely than males.

The reasons for the more rigorous thermoregulation achieved by the female snakes examined in the present study are, necessarily, purely speculative. However, Gibson and Falls suggested that being viviparous, female *T. sirtalis* are involved in numerous aspects of the production of young; the processes of vitellogenesis and embryogenesis and that the influence of the female over the rates at which these processes occur may be expressed in thermoregulatory precision. Furthermore, in male *T. sirtalis*, spermatogenesis takes place during

the summer and high temperatures may be detrimental to this activity.

Although no information is available concerning these processes in *N.a. humphreysi*, it seems probable that similar factors may be responsible for producing the same effect in terms of thermoregulatory differences between males and females, however slight these differences may first appear. The observation that the mean substrate temperature recorded in male subjects during the present study was 2.58°C higher than those obtained for female subjects further indicates the ability of female *N.a. humphreysi* for thermoregulating more broadly than males. It was observed in the present study that males maintained mean body-temperatures more closely related to mean environmental temperatures.

1.6.8 Relationship of Temperature to Body-size.

As is characteristic of much of the recent research oriented towards the thermal ecology of snakes, little attention has been given to the relationships of individual body-sizes to body-temperatures. Among the investigators who have treated the subject of temperature-relations in snakes, only Carpenter (1956) and Gibson and Falls (1979) have investigated the effects of body-size. Carpenter arbitrarily assigned three species of *Thamnophis* to two categories for the purposes of his analysis, the criteria were subjects measuring over 300 mm and below 300 mm (based on snout-vent lengths). Although smaller snakes exhibited slightly higher temperatures in two of the species examined and lower temperatures were recorded in smaller snakes of a third species, Carpenter concluded that no significant difference existed with respect to the results. Gibson and Falls also concluded from their investigation that "there is no relationship in either sex between snout-vent length and body-temperature."

The present study suggests that in *N.a. humphreysi*, a slight tendency is evident for smaller individuals to have higher body-temperatures than larger individuals. This trend is shown in Figs. 23a and 23b. However, if the scores are arbitrarily assigned to categories as was done by Carpenter, eleven subjects < 1300 mm yield a mean body temperature of 23.2°C and fifteen subjects larger than

1300 mm yield a mean of 25.2°C. The analysis shows that on the basis of this interpretation, larger individuals maintain higher mean body-temperatures by an order of 2.0°C. However, if the weights of subjects are also arbitrarily divided into categories <1,000 g and greater than 1000 g the values of the means are 27.8°C and 25.2°C respectively. This indicates that lighter subjects had higher mean body temperatures by an order of 2.6°C. The results suggest that the arbitrary assignment of weights and lengths into two classes cannot be regarded as an efficient method of assessing temperature-size relationships in these animals.

Gibson and Falls (1979) stated that male *T. sirtalis* are smaller, in terms of individual size, than females of that species and they exhibit lower body temperatures; consequently, techniques of combining data from both sexes in a single sample may produce a methodological artifact, introducing a spurious positive association to the relationship between body-temperature and body-size. In the present study, mean body-lengths of the *N.a. humphreysi* males (132.2 cm) were very similar to those of females (131.5 cm) but the mean weights of males (881.8 g) differed greatly from those of females (1130.0 g.). However this study has also shown that the difference in body-temperatures is slight and that the slight tendency for smaller animals to have higher temperatures is evident when both the length and weight of the subjects is compared. Further to this, it should be noted that although subjects were captured unsystematically, it was observed that larger animals tended to be captured under slightly warmer conditions than smaller animals, although this difference was very slight. If any bias with respect to sex-weight relationships occurred in favour of the larger females which have higher body-temperatures, the trend may be expected to develop in the opposite direction than that evidenced from Figs. 23a and 23b.

In the two previous studies discussed above, the investigators have treated the snout-vent lengths of the animals as being generally representative of body length. However, in the present study total body lengths of individual snakes were related to body-temperatures. Whether this difference has any effect on the final assessment of the pertinent differences is not known.

1.6.9 Site-related Differences in Biomass.

The results given in Table 7 and also illustrated in Figs. 27a and 27b clearly indicate differences in the biomass of *N.a. humphreysi* recorded at Brownwater Lagoon and Silverplains Creek. In determining the ecological significance of these differences in biomass between sites which are only eight km apart and are at the same elevation, several factors should be considered. Firstly, the relatively constant abundance of potential prey-species at Brownwater Lagoon, contrasting with the fluctuating supply of prey at Silverplains Creek may be important. It was observed that the creek is literally flushed clear of small frogs and lizards over the winter months, leaving very few breeding animals to re-populate the area when the level of the water in the creek subsides and only small pools remain. It appears reasonable to assume, therefore, that the population of frogs may be effectively maintained at a ceiling by the predators which prevent the prey from attaining large size or to increase to substantial numbers.

By comparison with Silverplains Creek, the population of frogs at Brownwater Lagoon increases considerably during the quiescent season of the snakes and breeding of the prey is not interrupted or impaired by the rising of the water level of the lagoon. In fact, the filling of the lagoon provides breeding facilities for the frog populations in the Brownwater Lagoon area. The substantial increase in the numbers of frogs is accompanied by the opportunity for them to attain maximal size as well as high population density. This provides the predators with increased possibility of food intake in relation to the energy expended, than at the Silverplains Creek study site.

Although home-sites of *N.a. humphreysi* are relatively plentiful along the perimeter of Silverplains Creek, the availability of home-sites for prospective prey-species is scant compared to the study-site at Brownwater Lagoon. It appears that the dry creek-bed at Site II provides a disproportionately large number of home-sites for prey-species during the dry-season. In the course of the wet season, frogs may retreat to the high ground near the marshy area at the northern perimeter of the creek. If this is the case, the prey-species may have to migrate back into the creek proper as the bed of the creek becomes drier and only still pools remain. A high density

of tadpoles in the pools along the creek bed suggested that most of the breeding-activities of frogs occur there. If this situation prevails, it seems reasonable to assume that a slow "filtering" of frogs, from the high ground down to the drying creek may occur during the early summer and the population of snakes at Silverplains Creek may not have access to a ready supply of prospective prey, unlike the Brownwater Lagoon population.

During the course of investigations it was noted that the population of *N.a. humphreysi* at Silverplains Creek was more exposed, or likely to be subjected, to culling by human activity within the area. During the summer, the Silverplains area is the site of a considerable amount of human recreational activity and open seasons on wallaby, trout and deer all occur within a period of two months. This results in the presence of large numbers of hunters, coming into contact with and subsequently killing a relatively high proportion of the snake population at Silverplains. The probable effect of this form of adventitious control is that the decline in the snake population (at least the larger, more conspicuous individuals) at the Silverplains Creek study-site creates a situation whereby immigration of snakes from less productive (in terms of abundance of prey-species) areas may and probably does occur. If this premise is correct, the snakes from relatively impoverished areas may be expected to be less robust than those occurring at study-site II, where the abundance of prey-species is high. Alternatively the smaller and/or younger individuals of the population at Silverplains Creek may take advantage of, and utilize the vacant home-sites created by the culling of larger, more conspicuous individuals.

With respect to sex ratios, the population at Brownwater Lagoon contained a higher proportion of females to males than the population of Silverplains Creek. Since female snakes at both study-sites were heavier than males (Section 1.6.8), this factor alone may account for the recorded differences in biomass. Although no females were dissected to determine gravidity, reproductive rates may have been higher at study-site II than at study-site I, possibly because of the clumped pattern of population-dispersion and/or the better prevailing conditions, in terms of prey-species abundance and culling-pressure via human activity.

1.7 SUMMARY

The major aims of the investigation of the ecology of *N.a. humphreysi* undertaken in the present study were to examine, under natural conditions, the relationship of the animals to specific environmental factors operating within this habitat. After recording the relevant environmental temperatures and body-temperatures, the relationships between these variables were examined. With respect to thermal ecology, the relationship between percentages of cloud-cover and the activity levels of the animals and their body-temperatures were investigated. The relationships between the sex of individuals and their body-temperatures were also examined as was the relationship between their body-size and body-temperature. The final temperature-relationship to be examined was the effect of relevant environmental and body-temperatures on the activity status of the subjects.

Observations were made in the field and these permitted investigation of diurnal variations in the general activity of *N.a. humphreysi* as well as the relative abundance of the animals within the study area, their spatial distribution and relative habitat-utilisation. Speculations were also formed concerning the factors affecting the above variables. Comparisons were made of the differences in structure, between the snake populations at two defined study-sites and inferences were subsequently made concerning the possible reasons for their existence.

Particular attention was given to the problem of the utilization and maintenance of home-sites by *N.a. humphreysi* and several distinctive characteristics, associated with tenure of permanent home-sites, were identified.

CHAPTER 2

DIRECT OBSERVATIONS CARRIED OUT UNDER NATURAL CONDITIONS

2.1 POSTURAL CHANGES AND RELATED BASKING BEHAVIOURS

During field-investigations on *N.a. humphreysi*, over 50 individual specimens were observed and their activities recorded while they were pursuing locomotory activities or laying still, with intermittent postural changes. Of these subjects, twelve were maintained under observation for a period extending for a brief duration after emergence, while carrying out locomotory activity at a distance from the home-site and subsequently returning to their home-sites. These animals exhibited distinctive types of behaviour, somewhat stereotyped in expression, during periods of activity which occurred directly outside the burrow or home-site entrance.

i) Post-emergence basking posture

In all recorded instances, the subjects assumed a tightly-coiled posture after emergence from the entrance of the home-site. This posture consisted of coiling the body in a circular manner, with the ventral surface against the substrate, until the body was completely coiled and the head was positioned across the dorsal surface of the body, facing away from the entrance of the home-site. Fig.28(a) illustrates a typical instance of the tightly-coiled posture, which was invariably adopted while the snake was resting on the post-emergence basking-pad described in Section 1.5.1, and Fig.12. After varying periods of time in the tightly-coiled posture, three of the subjects assumed the loosely-coiled posture illustrated in Fig.28b. This posture was achieved by a loosening of the body coils and changing the position of the body so that it was no longer in a circular configuration. The head was positioned across the dorsal

FIG. 28 TYPICAL BODY-CONFIGURATIONS (INTENSITIES OF COILING) OF
N.A. HUMPHREYSI AT THE ENTRANCE OF HOME-SITES.



(a) Tightly coiled posture.



(b) Loosely coiled posture.

surface of the body, facing away from the entrance of the home-site. Precise durations of the maintenance of these basking postures were not recorded, because it was presumed that these would be related to temperatures which could not be accurately recorded as the observer was required to maintain some distance from the micro-habitats of the snakes during observations.

ii) Pre-foraging basking behaviour

Immediately before a subject moved away from the home-site, the body configuration was changed to the half-loop posture illustrated in Fig.29a and 29b. The subjects achieved this posture by moving out of the coiled position, forming a single loop of the body, and orienting both the tail and the head towards the entrance of the home-site. In Fig.29a the head and tail are equidistant from the home-site entrance, whereas in Fig.29b the tail is extremely close to the entrance of the home-site and the head is facing back along the body toward the entrance of the home-site. Although slight variation in the proximity of the head and tail to the entrance of the home-site occurred, in this posture both the head and the tail were invariably oriented toward the home-site entrance, with the body configuration being a half-loop. This "shuttling" sequence of behaviour was exhibited by all twelve of the subjects observed systematically. However, in the course of four other observations the snakes were noted to return to the home-sites after they were recorded to rest in the post-foraging posture. It is not known whether the animals were disturbed by the presence of the observer during any of these four episodes, or not.

While snakes adopted the loosely-coiled posture and, particularly, the looped-posture an additional component, consisting of a dorso-ventral flattening of the anterior parts of the body was observed. In some cases flattening of the entire body (except the head and tail) occurred. During attempts at capturing specimens, it was noted that snakes resting in a coiled posture could be approached more easily by the observer (apparently without being noticed), than those in a looped posture; consequently, it may be assumed that animals adopting a looped-posture may have been more alert or capable of more rapid response than those that were coiled.

FIG.29 CHARACTERISTIC PRE-FORAGING POSTURES OF *N.A. HUMPHREYSI*.



(a) Extremities equidistant from the entrance of the burrow.



(b) Extension of the body from the entrance of the burrow.

2.2 FORAGING BEHAVIOUR

After leaving their home-sites, the animals generally began to move over the surrounding vegetation and/or rock-outcrops. It was considered that this activity was related to the procurement of food, and was consequently termed foraging behaviour. Durations and the distance moved in the course of this activity varied and are presented in Section 1.5.2.

As snakes moved away from their home-sites, they usually began probing with their muzzles around the perimeter of rocks and fallen timber, close to the substrate. The probing-actions consisted of forcing the snout into hollows of suitable dimensions beneath obstacles close to the surface. If the snake was unable to insinuate its muzzle into an opening, it subsequently withdrew the anterior end of its body from the site and continued to probe systematically around the object. During periods of this activity, tongue-flicking was regularly and constantly performed; however, while the snake was moving from one obstacle to another, the frequency of tongue flicking was substantially reduced. The terrain utilized by the animals in the course of foraging activities, varied considerably from rocky creek-beds to open grassland and dense vegetation. An example of foraging in the latter type of habitat is given in Fig.30.

On some occasions, when a snake succeeded in entering an opening beneath a rock or timber, the amplitude of the coils of the body near the anterior end was increased. The snake appeared to gain anchorage against the substrate by adposing the posterior part of the body to the surface of surrounding rocks, timber or tussocks. The anterior region of the body was continuously driven forward into the opening. Thereafter, one of two characteristic sequences of behaviour were observed; the snakes either (a) retracted the body from the opening and continued to forage or, (b) the tail contracted briefly and spasmodically and the anterior of the body was thrust forward.

Snakes generally withdrew from the opening shortly (within 1-5 min) after the forward thrust had been effected. Individuals were observed to perform sequences of "yawning" or gaping of the mouth

(as described in Section 3.3.2g) on six occasions after emergence. An example of post-withdrawal "yawning" is illustrated in Fig.31. During the episode shown, the snake had entered an opening beneath a layer of debris, over which the anterior part of its body was resting. The posterior part of the body was positioned in contact with fallen timber during the performance of the forward thrust.

Foraging appeared systematic because each obstacle was meticulously searched around its perimeter, before the snake moved further to the next obstacle. In some instances, snakes foraged in a circular pattern around their home-sites before moving outside the range of vision of the observer or returning to the home-site. The precise expression of the foraging activities appeared to depend on the features of the particular habitat. For example, at Site II (Silverplains Creek), the following general foraging pattern was observed:

The snake moved away from a home-site, situated under a rock some two m from the border of the creek, and commenced foraging after it had entered the dry bed of the creek. The banks of the creek were approximately one m high. As the snake continued to forage, it moved along one side of the bed of the creek probing under stones and fallen clumps of soil, for a distance of four m. The animal then traversed the centre of the bed of the creek (a width of two m) and continued foraging, in the opposite direction, along the creek-bed. When it reached the site of its initial entry to the creek, it moved over to the opposite bank and foraged (upstream) for a distance of four m. The snake subsequently ascended the bank of the creek and foraged in the reverse direction (downstream), along the grass-covered bank of the creek, continuing for another four m past the position of its initial entry. This systematically performed sequence of activities was then repeated downstream from the home-site until the animal returned to the latter. The entire period of foraging required one and one-quarter h and during the course of these activities, the snake moved over a distance of 36 m.

In some instances animals were observed to cease foraging, thereafter resting motionless in contact with the substrate, with the body partially flattened (dorso-ventrally). This posture was

FIG.30 ACTIVITIES ASSOCIATED WITH FEEDING BEHAVIOUR.



Foraging among fallen timber.

FIG.31 POST-WITHDRAWAL (FROM BURROW) BEHAVIOUR.



Elevation of the head and yawning after ingestion of prey.

not maintained for more than thirty minutes in any given episode before the snake resumed its foraging activities.

This postural change was expressed more often when the animal was moving over rocky terrain, particularly the creek-bed at Silver-plains. On one occasion, an individual was observed to halt its forward progress and dorso-ventrally flatten the anterior of its body on a small patch of grassland, where the rays of the sun had penetrated through the tree canopy. This occurred at the Brown-water Lagoon study-site.

2.3 INVESTIGATION OF PREY-SPECIES

During field investigations on *N.a. humphreysi*, analysis of the contents of the alimentary canal for identifying the presence and proportional representation of various species of prey was restricted to road-kills collected from the study area. No specimens were killed for this purpose in order to ensure that sufficient numbers of snakes remained at the conclusion of the field-investigations for *in vitro* observations on feeding behaviour.

A total of eleven fresh road-kills were examined in the course of analysis of the contents of the alimentary canal and the results of this may be summarised as follows:

<u>Subjects</u>	<u>Species of Prey</u>	<u>Number (individuals) Present</u>
1		Nil
2	<i>Litoria ewingi</i>	3
3	<i>L. ewingi</i>	1
4	<i>L. ewingi</i>	3
5	<i>L. ewingi</i>	2
	<i>L. raniformis</i>	1
6		Nil
7		Nil
8	<i>L. ewingi</i>	4
9	<i>L. ewingi</i>	1
10	<i>L. ewingi</i>	2
11	<i>L. ewingi</i>	2

Of the total number (nineteen) specimens of prey located, 97% comprised the frog *L. ewingi* and 5.3% were of the frog, *L. raniformis*.

It was considered that since two species of frog were found in the alimentary canal of *N.a. humphreysi*, other animals of similar size and occupying similar microhabitats would also be prospective prey-species. Assessment of the frequency and abundance of potential prey-species at Site 1 was attempted by systematically overturning logs and stones at intervals around the perimeter of the

lagoon where *N.a. humphreysi* were seen to forage. This was done in the course of three field-exercises on 30/4/1981, 18/7/1981 and 8/11/1981. By using these methods it was possible to obtain an indication of any recruitment or depletion in the abundance of potential prey-species, during periods when the intensity of feeding activity by the predator was relatively low.

The possible prey-species found in Site 1 were as follows:

- 1) *Leolopisma metalicus*
- 2) *Crinea signifera*
- 3) *Lymnodynastes dumerilli*
- 4) *Litoria ewingi*
- 5) *Litoria raniformis*
- 6) *Leolopisma entrecastrauxi*

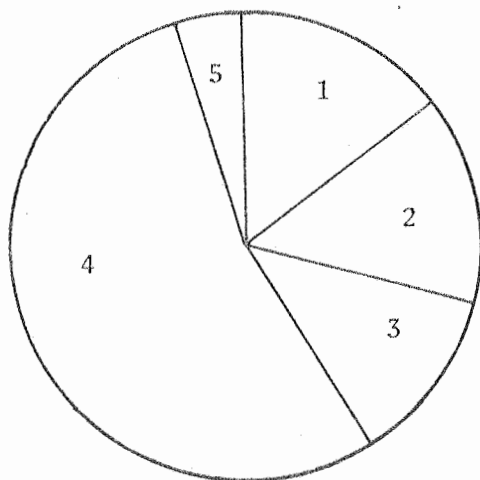
The sample results are given in Fig.32.

The reason for the decline in the proportion of *L. ewingi* present at Brownwater Lagoon on the sampling date 18.11.1981 was mainly that the lagoon was filled with water and the frogs had moved outwards into the reeds and small island, probably to commence breeding. Their presence was rendered conspicuous there by their continual vocalizations, recognised as being produced by all of the recorded species, and performed at a consistent and characteristic frequency during the day. In the course of this particular recording session, two large specimens of *N.a. humphreysi* were observed foraging on high ground at a distance approximately four m from the margin of the lagoon; this occurred notwithstanding the fact that the great majority of frogs were in the lagoon proper.

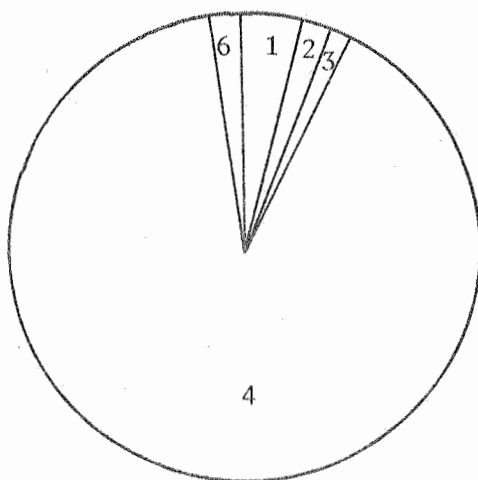
Sampling for prospective prey-species at Silverplains Creek was accomplished on 30.4.1981 by turning over stones on the bed of the creek in 1m² quadrats examined at ten m intervals along the length of the creek. A total of 50 quadrat-samples produced a yield of 218 *L. ewingi*, 61 *C. signifera*, 50 *L. dumerilli*, and 14 *L. raniformis*. A second sampling-session, undertaken on 18.7.1981 was unsuccessful, since the creek was full of rapidly flowing water. A systematic search of the fallen timber around the creek banks revealed that only small numbers (<10) of most species of frogs were present and *L. ewingi* numbered only 57 individuals. A similar non-quantitative in-

FIG. 32 PROPORTIONS OF POSSIBLE PREY-SPECIES COLLECTED AT SITE 1.

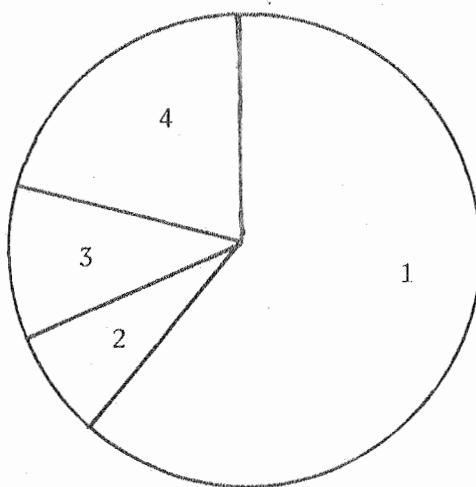
30-4-1981



18-7-1981



8-11.1981



vestigation was performed on 8.11.1981 with similar results, i.e. *L. ewingi* was the most abundant species of frog present and other species were represented in smaller numbers.

2.4 DISCUSSION

It has been previously documented by Spellerberg (1972), Hamerson (1979), Heatwole and Johnson (1979) and Lillywhite (1980) that several species of thigmothermic, squamate reptiles perform series of postural changes and associated movements in the course of thermoregulatory behaviour under both natural and laboratory conditions. Heatwole (1976) stated that "the amount of energy received from the sun by a unit area of surface depends on the angle at which the sun's rays strike that surface. Because of this phenomenon, a reptile can regulate its heat absorption by changing its angle of incidence to the sun's rays".

In addition to influencing the angle of incidence to radiant energy, postural adjustments may be used to change the actual amount of surface-area exposed to the sun. Heatwole (1976) observed that many species of reptile flatten their bodies when cool and in the presence of sunlight, thereby exposing a larger area of their surface to the sun than would occur if other postures were maintained. The results of the present study suggest that *N.a. humphreysi* may change its body position as well as its body composition, during thermoregulatory behaviour.

Both the tightly-coiled and loosely-coiled postures that were adopted by snakes following their emergence from the burrows or home-sites were highly characteristic, in all observed instances, of the post-emergence basking behaviour. The coiling of the body is a potential means whereby the snake can reduce the surface area from which back-radiation can occur and heat-loss can therefore be reduced, if the body-temperature of the animal is higher at the time of emergence than that of the surrounding environment (Heatwole, 1976). These postures probably also assist in warming the body of the snake during basking, by a reduction of the surface exposed to the environment and consequently to back-radiation. The same process of "early warming-up" by basking has also been documented by Lillywhite (1980) in *N.s. scutatus*, *P. parphyriacus* and *P. textilis*, observed under laboratory conditions.

Using an experimental approach, Lillywhite was able to determine that each of the snakes tested elevated its body temperature by warming itself (basking) under a heat-source. Thereafter they maintained

a relatively narrow range of elevated body temperatures during subsequent activity, within the thermal gradient of the enclosure. One specimen of *N.s. scutatus* exhibited an initial increase in body-temperature from 26°C to 33°C in the course of fifteen min during post-emergence basking. Lillywhite also found that while engaged in basking, snakes positioned their bodies in configurations which varied from fully extended to tightly-coiled. Adult specimens were occasionally observed to adjust their basking positions similarly to the postural changes observed in the present study.

The naturalistic observations recorded in the present study appear to be in substantial agreement with the laboratory-based experiments performed by Lillywhite and other investigators. The tightly-coiled posture is considered to be the most probable means whereby *N.a. humphreysi* can increase its body-temperature to a preferred foraging temperature with maximal efficiency and rapidity immediately following emergence from home-sites. This warming technique presumably reduces the time when the animal may be sluggish and vulnerable to predation.

The changes in posture and shuttling in and out of direct sunlight observed by Hammerson (1979), Heatwole (1979), and Lillywhite (1980) were also noted in the present study. The movement of a snake into a half-looped posture, before the onset of foraging, appears to indicate the attainment of optimal or near optimal body-temperatures for foraging, since in most instances the snakes moved off to forage shortly after adopting this configuration. The fact that some subjects were observed to return to their home-sites after assuming the half-looped posture may indicate that over-heating has occurred and a subsequent cooling period was required. Heatwole (1976) stated that "many reptiles seek shade when they overheat, and that repeated alternation between sunlight and shade (shuttling) is characteristic of many species".

During investigations of the thermal ecology of *P. parphyriacus* under laboratory conditions Heatwole and Johnson (1979) found that body-temperatures of the snakes was reduced as the animals entered shade and that the body-temperature increased again when the animals re-entered areas of direct sunlight. This is most probably also the case in *N.a. humphreysi* where movements in and out of the

home-site, represent alterations between sun and shade.

The flattening of the body during basking periods observed in *N.a. humphreysi* has also been recognised and described by Heatwole and Johnson (1979). As a result of studies on *P. parphyriacus*, these investigators found that "the cool snake enhances its heating rate by flattening and tilting but as it reaches the preferred range it undergoes behaviour that slows down the heating rate, i.e. assumes the normal rounded contour of the body". This type of thermoregulatory behaviour was observed while specimens of *N.a. humphreysi* were positioned immediately outside the entrance of the home-site, and intermittently also during foraging episodes.

The observations suggest that *N.a. humphreysi* has a similar range of behavioural adaptation to *P. parphyriacus* (in terms of thermoregulatory activity) and that body-temperatures are most likely to be reduced as the animal forages; consequently requiring brief periods of altered activity during which the snake can re-establish the body-temperature most suitable for foraging. Heatwole and Johnson (1979) suggested that as long as an active snake does not perform any marked thermoregulatory behaviour, it can be assumed that its internal temperature is maintained within the preferred range. The internal temperatures at which it initiates overt thermoregulatory behaviour may be regarded as marking the limits of the preferred values. Thus, the internal temperature at which the flattened posture is supplanted by exhibiting the normal, cylindrical contours of the body in a warming snake (or the reverse process in a cooling one) would seem to indicate the lower limit of its preferred range of body temperatures.

The relationship of the relative alertness of basking subjects of *N.a. humphreysi* while in the two major basking postures described suggests that the snakes are warmer, or closer to their optimal body-temperature, when resting in the looped posture than while adopting the initial coiled posture. The fact that in all instances when the looped posture was observed, the head and tail were directed toward the entrance of the home-site possibly indicates alertness or the presence of an escape-tendency to enter the home-site, should the snake be disturbed. Individuals adopting the coiled posture were, however, invariably closer to the entrance of their home-sites than

those assuming the looped posture (being on the post-emergence and pre-foraging basking pads, respectively) and therefore probably required to cover less distance in order to decamp to the home-sites. This probably compensated, at least partly, for the observed differences in body-temperatures associated with each posture. Furthermore in the coiled posture the head of the snake faces away from the entrance of the home-site, thereby possibly providing a better view of approaching danger than when the looped posture is assumed.

There is little documented information regarding the foraging behaviour of large Australian elapids. It has been shown by several authors (e.g. Henderson and Nickerson, 1976) that many colubrid snakes, particularly those living aboreally, typically do not forage actively for prey but tend to remain more-or-less motionless waiting for movement by their prospective victim. This also applies to the aboreal pythons and many other reptiles (Bellairs, 1969); the majority of these lie immobile until potential prey approaches, or stalk the latter for a short distance. Capture of the prey is subsequently effected by a lunge, strike or a sudden rush culminating in a snap or bite. Since large representatives of colubrids, crotalids and viperids are usually nocturnal or crepuscular, and their major food, or prey items are small mammals (Shine, 1979), it appears probable that these animals would either use techniques of ambush or overtly hunt for food, i.e. in open situations.

Shine (1979) suggested that, in accordance with the species of prey utilised by most elapid snakes of continental Australia, i.e. mainly lizards and frogs, these snakes are generalised searching foragers rather than nocturnal "ambush" predators.

The observations on foraging behaviour described in the present study were an attempt to obtain a general over-view of the animals activity routine in natural conditions. The probing activity or muzzling behaviour exhibited by the observed subjects clearly indicated that the intention of the activity was to enter, where possible, burrows beneath obstacles on the substrate. This hypothesis was further substantiated by the observation that the rate of tongue-flicking increased when the snakes were circumnavigating the perimeter of obstacles, compared to traversing terrain between obstacles. The importance of the rate of tongue-flicking in relation to feeding in

snakes has been well documented by Burghardt (1967 and 1968). Burghardt's investigations disclosed that the stronger the stimuli (feeding-response releases) the more rapid were the tongue-flicks. Thus, it can be postulated that subjects of *N.a. humphreysi* exhibit increased rates of tongue-flicking in response to, or in anticipation of, the reception of stimuli emanating from a suitable prey-species.

The post-withdrawal "yawning" (which is associated with feeding in snakes; Bellairs 1969) exhibited by several individuals during the period of observations further suggests that the purpose of entering the burrow and performing anchoring and forward-thrusting activities is to procure food. During the course of the entire observation period, not even a single instance of killing performed in the open by *N.a. humphreysi* was observed. The above factors, in conjunction with the fact that all obstacles in the path of the foraging predator were systematically searched, suggested that this species may accomplish the majority of its capture of prey within the confines of the burrow of the prey-species and not necessarily in open areas.

The proportion of road-kill specimens that contained prey-items in the alimentary canal was high when it was compared with ten elapid species dissected by Shine (1980). In these animals an average of 20.3% of snakes contained prey-items, whereas 72.7% of the *N.a. humphreysi* dissected in the present study contained ingested prey. By far the most important prey-species of the *N.a. humphreysi* examined in the Lake Sorell - Lake Crescent study area was the small frog, *Litoria ewingi*.

Although only eleven road kills were analysed, the high proportion of *L. ewingi* present in the alimentary canal suggests that this species of frog is most probably the major species of prey in the diet. The abundance of this frog species was evident when the late-summer and mid-winter samples contained a substantial amount of *L. ewingi* compared to the other species recorded in the area. These data also showed that over a period of almost three months the relative proportions of the prey-species available to the predator fluctuates, with an increase in the relative proportion of *L. ewingi* occurring during the winter months. This increase is probably due to the emergence of the frogs from deep burrows within the substrate or a migration from other areas to the lagoon for breeding activities.

It appears likely that because of the high level of breeding-activity observed at the lagoon during the field-study undertaken on 8.11.1981, a large increase in the population density of all species of frogs that were recorded occurs in early summer. The migration of frogs from the perimeter of the lagoon to the lagoon proper represents a loss in terms of readily available prey-species at the former site and this may result in *N.a. humphreysi* transferring its feeding-activities to species of lizard, such as *L. metalicus*, which are abundant at that time until the frogs return to the edge of the lagoon. Although the snakes observed in the field-study of 8.11.1981 were actively foraging on high, dry land it is possible that these animals are capable of hunting frogs in or around the confined spaces within the reeds at water level.

In comparison with the diet of elapids on the Australian continent prey-selection by *N.a. humphreysi* compares favourably with large snakes occupying similar habitats. Shine (1977) has shown that *N.s. scutatus* relies heavily on frogs as its prey-species. In one sample, 2.2% of the food items found within the alimentary canal were lizards whereas 92.2% were frogs. Dissections of *A. superbis* revealed an almost equal selection of frogs and lizards, and dissections of *P. parphyriacus* revealed a preference for lizards as prey. These data indicated that *N.a. humphreysi* has a diet more closely related to that of *N.s. scutatus* than to other large elapids so far investigated.

The gut analysis and sampling of prey-species both suggest that *L. ewingi* is the major species of prey utilized by *N.a. humphreysi* in the area examined and this species of frog is also the most abundant and, consequently, the most readily available food-source, since it normally occupies shallow burrows with a single entrance and the opportunity for escape is limited (personal observation).

2.5 SUMMARY

The series of direct observations made in the field were aimed at examining several of the behavioural traits exhibited by *N.a. humphreysi* during daily activity periods. Basking behaviour, associated with the characteristics of the permanent home-site, was examined in detail as were the activities performed by the animals during bouts of foraging. The importance of basking behaviour, in relation to thermoregulatory behaviour was examined together with an assessment of the significance of the behavioural events occurring during bouts of foraging.

An investigation was made into the prey-species utilized by *N.a. humphreysi*. The abundance, seasonal fluctuation in numbers, and general habits of possible prey-species are examined.

CHAPTER 3

FEEDING BEHAVIOUR

3.1 INTRODUCTION

For the purpose of the present investigation, feeding behaviour refers to the terminal sequence of behavioural events exhibited by a foraging predator following an encounter with a suitable specimen of prey, and includes the capture of prey, its manipulation and ingestion. These behavioural categories comprise the concluding chain of events involved in the general phenomenon of predation. Curio (1976) defined predation as "a process by which an animal spends some effort to locate a live prey and, in addition spends another effort to mutilate or kill it".

Since predation and feeding behaviour accounts for a high proportion of the time a predator spends in the course of its period of activity, this aspect of the ethology of active carnivores has received a considerable amount of attention from investigators in the past. The feeding behaviour of many taxa of animals, both vertebrates and invertebrates, have been the focus of investigations at one time or another. A comprehensive reference list of such studies is provided by Curio (*op cit.*).

Documented research pertinent to the aims of the present investigation are scarce and the majority of studies on the predatory and feeding behaviour of reptiles have concentrated on various species of lizards (e.g. Burghardt, 1964; Goodman, 1970 and Loop, 1974), constrictors (e.g. Ulinski, 1972; MacDonald, 1973 and Willard, 1977), or North American species of colubrids (e.g. Burghardt, 1967 and 1968; Burghardt and Hess, 1968; Burghardt and Abeshaheen 1971; Greenwald 1974 and Chizar, 1976). Surveys by Van Riper (1953),

Gans (1961) and Kardong (1975), have served to reveal deficiencies of detailed studies of the feeding behaviour of large, venomous snakes; most of the early attempts at investigating these have centred upon the striking and biting-mechanisms.

Kardong (1975) was able to elucidate the events preceding actual captures, as well as the striking and biting actions of the cotton-mouth snake *Agkistrodon piscivorus* by means of high-speed cinematography. Similar techniques were employed by Greenwald (1978) in a study of prey capture by Sonora gopher snakes *Pituophis melanoleucus affinis*, in an attempt to determine the distinctive behavioural elements occurring during feeding in laboratory conditions.

The principal aims of the present study were to investigate the temporal relationships and kinematics of prey-capture in *N.a. humphreysi* observed under controlled laboratory conditions and to apply more naturalistic situations, in order to assess the ecological significance of the behavioural events identified. The methods were intended to provide information from *in vitro* investigations, supplemented by direct field-observations of foraging behaviour, in order to gain a comprehensive view of relevant daily activity patterns of the animal.

3.2 MATERIALS AND METHODS: A General Description

During April 1981, ten specimens of *N.a. humphreysi* were captured and removed from the Lake Sorell study-area for the purpose of direct behavioural observations. These animals were housed in a segregated laboratory, approximately 10m x 3m x 3m in dimension. Eight of the subjects were maintained individually in boxes 30cm x 60cm x 30cm, opening from a fly-wire roof and containing hessian mats, to represent ground cover, as well as water-bowls. Each box was individually provided with a 40-watt electric light-bulb, to provide both heat and light, connected to a time clock. Two large individuals were housed together in an enclosure of 50cm x 150cm x 50cm, containing the same range of items as the other cages. The light-bulbs were scheduled to commence functioning at 0800 h for ten h daily, until 1800 h. The range of temperatures fluctuated between 20C⁰ and 25C⁰ within the boxes throughout the daylight period, and were as low as 2C⁰ overnight. It was considered that these variations resembled the actual conditions experienced by the snakes in natural situations.

The subjects used in the study ranged in length from 1.23 m to 1.51 m and their weight varied from 980 g to 1,500 g. Five subjects of each sex were investigated. Individuals were selected for observation randomly during all experiments, thereby eliminating possible bias due to length-weight or sex differences. These individual variables were not examined, since the experiments were aimed at obtaining a generalised over-view of the habits of the animals rather than length-weight or sex specific characteristics. Food was supplied once weekly in the form of a single live laboratory mouse (*Mus musculus*) for each snake, and the water was changed once a week in the course of routine cleaning operations.

3.3 EXPERIMENTAL SERIES 1 : PREY-CAPTURE AND ASSOCIATED ACTIVITIES IN A SPECIALLY DESIGNED OPEN-FIELD ARENA

3.3.1 Materials and Methods

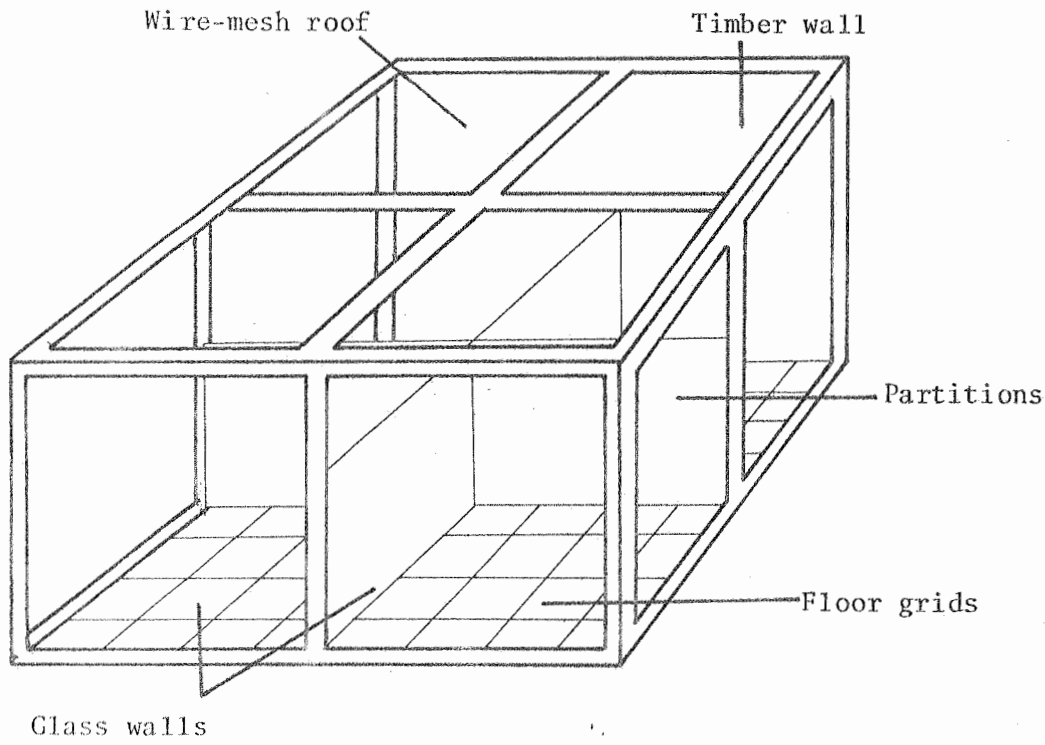
The equipment used for the first series of experiments consisted of an observation-arena measuring 2m x 2m x 1m (Fig.33). This consisted of three glass walls, one timber wall and doors opening at the roof, composed of fly-wire. The arena was painted neutral grey and was partitioned into four one metre areas. The floor was transected by 12.5cm grids applied with black ink. Lighting was provided by a single 100-watt electric light bulb, suspended in the centre of the arena, from its roof. Heating was additionally supplied by four strip-heaters (each having two elements) secured to the roof of the arena between the frames of the doors. The heaters were connected to a voltage-flow controlling mechanism to permit regulation of ambient temperatures. During the experiments the temperature of the arena was maintained at 25°C - 30°C , monitored by means of a thermometer positioned on the floor, in the centre of the arena.

Recording equipment consisted of a stop-watch, a mechanical (manually operated) event-counter, and a National-WV-3085 portable television video-camera. The video-camera records of the activities of the subjects permitted accurate identification of specific events when analysed on the television screen. The rate of exposure obtained with the camera was sixteen frames /s. Images were traced directly from the screen of the television and converted to frame-by-frame illustrations of the typical sequence of prey killing. In an attempt to supplement these, a sixteen mm Beaulieu R-76 cine-camera, with a rate of exposure of 80 frames /s, was also used during some of the experiments. This was suitable for high-speed analysis of the duration and accuracy of striking. All photographic exposures were obtained from an overhead position, 1.5 m directly above the floor of the arena.

Several variables were considered to be of particular importance in analysing prey-killing and feeding behaviour and these were selected for detailed examination. The categories were:

- i) Striking range (the distance of the anterior border of the muzzle of the snake from the nearest surface of the prey when the strike

FIG.33 OBSERVATION ARENA USED IN EXPERIMENTS I & II.



is released); ii) the orientation of the bite to the body of the prey; iii) the period (latency) to the death of the prey, following envenomation; iv) hooking, (characteristic lateral movements of the anterior part of the snake after striking the prey); v) release (relinquishing the grip on the prey after striking); vi) dragging (drawing the prey over the substrate after striking); vii) ingestion time, (the duration of ingesting the prey), and viii) orientation of the act of ingestion (whether prey were eaten from the anterior or posterior end first). Summarised records of these variables, obtained for individual sequences of prey-capture are presented in Table 8.

The experimental procedure used in the first tests consisted of introducing a single snake into one of the 1m^2 arenas after the arena temperature had reached approximately 28C° and remained constant at that level. The subject was then allowed a standardised acclimation period of twenty minutes before prey (one mouse) was introduced into the centre of the arena. Recording began immediately after the prey was placed in the arena. Adult laboratory mice (*Mus musculus*) were used as the prey species in this series of experiments. They were chosen because of their relative abundance, ready availability and fecundity. The snout-vent lengths of individual prey-subjects ranged from 8-10 cm.

3.3.2 Results

3.3.2a Search Behaviour and Associated Locomotory Activities

When first introduced into the arena, snakes generally moved around the central localities, characteristically exhibiting protracted bouts of tongue-flicking. These actions involved protruding the tongue, to what appeared to be its complete extension, and "waving" its bifurcated tip in a slow up-and-down motion, subsequently withdrawing the tongue. The entire sequence of protrusion to withdrawal of the tongue usually ranged from periods of two to three s. During all of the observation trials snakes performed wall-oriented activities around the perimeter of the enclosure. At the completion of the twenty min acclimation period, 30 of the 40 subjects that killed prey were observed to adopt a pre-foraging posture (a loosely-coiled or looped posture, also described in Section 2.1) in the corner of the arena, directly under the light-source. The remaining ten individuals were still actively pursuing investigatory behaviour after the twenty min period had elapsed. Investigatory behaviour within the arena consisted of probing the edges of the arena, with the muzzle, as the snake moved about near the junction of the wall and the floor. This type of behaviour was invariably accompanied by prolonged tongue-flicking activity.

When a mouse was introduced into the centre of the arena, at first it usually remained stationary, with the hind feet firmly planted on the substrate and the trunk extended *in situ* while it appeared to sniff the air (with relevant muzzle movements). After a brief period of time (generally not exceeding five min) the mouse usually moved towards the wall of the arena and commenced walking around the intersection of the walls and the floor. During this behaviour, mice regularly sniffed the floor, wall and air, halting intermittently to groom for short periods (generally less than fifteen s).

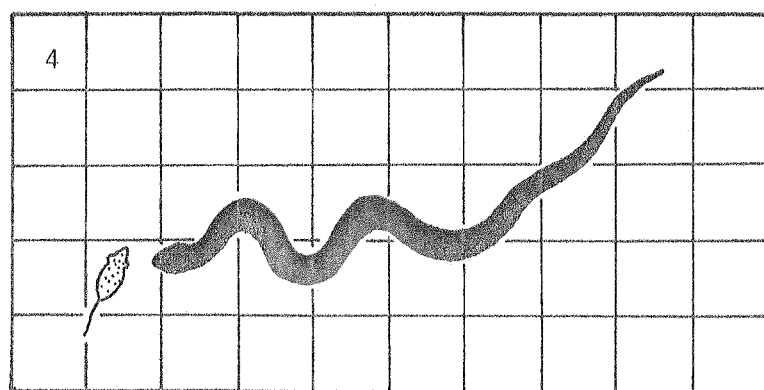
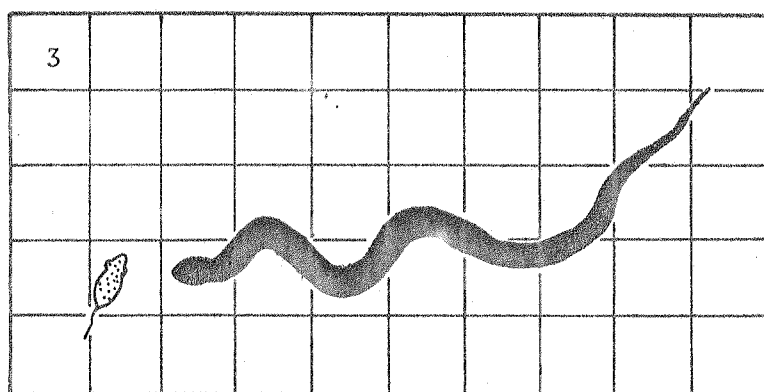
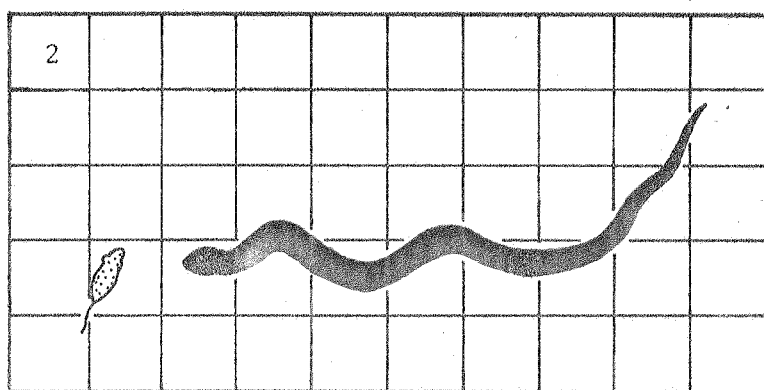
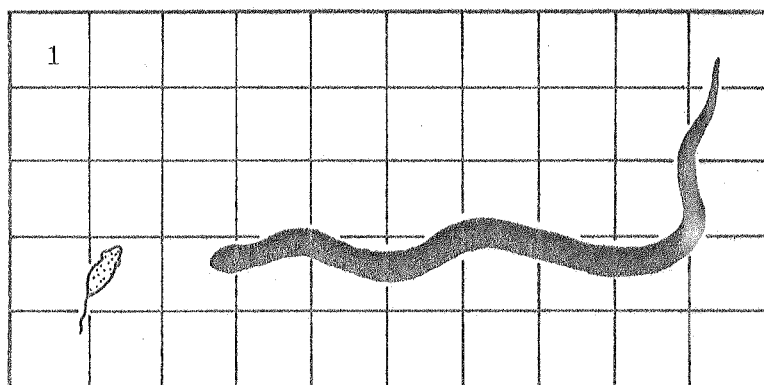
The greatest distance at which a snake appeared to become aware of the presence of its potential prey was 50 cm, and the shortest distance at which a mouse was detected was ten cm. Awareness of the mouse was indicated by characteristic behaviour of the snake, specifically the cessation of body-movements and a distinctive

orientation of the head towards the mouse. This was accompanied by a change in the frequencies of tongue-flicking to a form of activity that may be described as repeated tongue flicks. These were distinguishable from the prolonged tongue-flicking previously mentioned, in that the period from protrusion to withdrawal of the tongue was greatly reduced. During repeated tongue-flicking, the duration of the complete sequence of actions ranged from <0.5 to one s. and each "set" of repeated tongue-flicks contained three to five protrusions and withdrawal components. These series of actions (sets of tongue flicks) occurred at varying intervals, from ten seconds, (when the snake first became aware of the presence of the mouse) to two seconds (immediately before striking was released).

Snakes usually approached mice with slow, intermittent movements rather than in a smooth forward motion, and locomotion occurred as a series of forward-shunting movements. As the snake neared the prospective prey, the amplitude of the coils of the body, particularly those of the anterior part, gradually increased. Fig.34 illustrates the approach-technique employed by *N.a. humphreysi* and observed in the series of experiments described here. During this approach phase, mice usually exhibited two distinctive types of behaviour. In the majority of episodes, they remained stationary, without discernable movement of the body, until the strike occurred. The other form of behaviour consisted of directed withdrawal - i.e. the mouse sniffed in the direction of the snake, then turned and moved away from the approaching predator.

When a snake was within ca. ten cm from the potential prey, the head and the first loop of the anterior of the body were elevated from the substrate to a height of approximately one to two cm. Tongue-flicking occurred throughout the approach phase of the encounter.

FIG. 34 APPROACH TECHNIQUES EMPLOYED BY *N.A. HUMPHREYSI* PRIOR TO STRIKE RELEASE.
Each frame represents a time lapse of ten seconds.
Numbers indicate frame sequence.



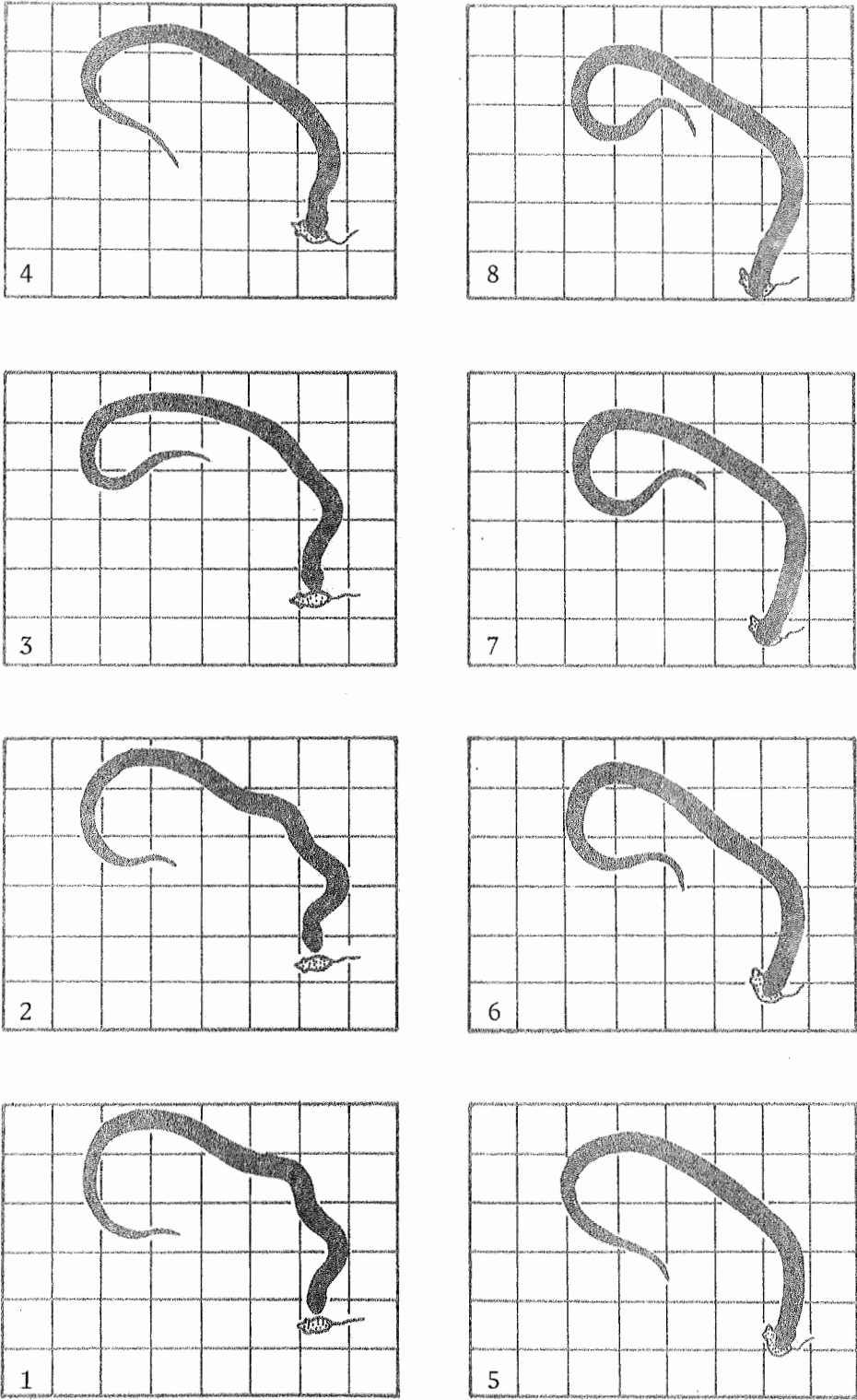
3.3.2b The Release and Kinematics of the Striking Response

When the head of the approaching snake was within a distance not exceeding five cm from its potential prey, it was vigorously thrust forward in the direction of the mouse. This action, which constituted the definitive strike, was accompanied by the uncoiling or extension of the two loops of the body situated immediately posterior to the head. A mean proportion of 12.50% of the total length of the body of the attacking snake was utilized in producing the strike by this means and in twenty episodes of killing, performed by ten snakes, the length of the body comprising the first two loops ranged from 8% to 20% of the total length of the body. The distance moved by the head of the snake during the strike-sequence also varied somewhat, depending on the type of technique employed. Successful strikes, leading to capture of the prey, occurred only when the distance from the anterior border of the muzzle of the snake to the prey was five cm or less. If the prey was further away than this when the strike was released, the attempt at capturing it invariably failed.

The snakes exhibited three types of distinctive behaviour during strike-sequences. These were:

- i) Forward-thrusting - consisting of propelling the head with considerable vigour in the direction of the strike, following contact with, and capture of, the prey. As Fig. 35 illustrates, the prey is forced along the substrate, in the direction of the strike, immediately after it is captured and, in fact, the forward-thrusting action actually appears to be an incidental consequence of the striking motion. The principal elements evident in this form of behaviour were the forward-thrusting and upward-arching of the first ten cm, or so, of the body of the snake. This arching produced an upward loop at the extreme anterior end of the body of the snake and, as a consequence, the prey was forced onto the substrate while within the grip of the snakes jaws. The forward-thrusting sequence occurred in only two (4.5%) of the 45 strikes observed.
- ii) Hooking - The term hooking may be applied to the technique by which a snake accompanies the strike by thrusting the head, to either side so that the configuration of the anterior part of the body resembles a simple loop or hook, while the ventral surface of the body

FIG. 35 FORWARD-THRUSTING TECHNIQUE EMPLOYED BY SUBJECTS AS A FOLLOW-THROUGH TO A SUCCESSFUL STRIKE.
 Each frame represents a time lapse of 0.25s.
 Numbers indicate frame sequence. Grids = 12.5cm.



is maintained in contact with the substrate. This action occurred in 95.5% (43 of 45) episodes of successful killing recorded. The intensity (degree) of hooking varied from the head facing toward the posterior of the body accompanied by a single semi-circular loop of the anterior part of the body (Fig.36), to a more elaborate lateral, coiling posture such as that shown in Fig.37. Arching of the anterior portion of the body occurred in all trials. Rolling of the head and anterior regions of the body were also performed at varying intensities on occasions when successful killing was observed. The rolling component accompanied the hooking actions and consisted of rolling the head toward the outside (convex) border of the hook. Fig.38 illustrates the rolling action associated with the hooking technique.

iii) Unsuccessful attempts at prey capture - When the head of a snake was situated at a distance exceeding five cm from the prey at the time when the strike was released, the attempt to kill was invariably unsuccessful. On such occasions, the snake usually either, a) pursued the mouse if it had not retreated beyond the range of another strike (five cm or more) or b) returned to the pre-strike posture (described in Section 3.3.2a) and continued to exhibit repeated tongue-flicking behaviour. Unsuccessful strikes appeared to be a consequence of inaccurate orientation by the snake rather than the simple fact that the mouse was physically outside the effective range of attack. This was evident from two salient observations. Firstly, in some unsuccessful attempts at striking, the snake actually contacted the mouse with its muzzle, then prodded it away without effecting a bite; secondly, in the majority of observed instances of unsuccessful strikes, the strike was directed over the dorsal surface of the mouse, or to either side without making contact.

FIG. 36

SINGLE, SEMI-CIRCULAR LOOP POSTURE EXHIBITED BY SUBJECTS
AS FOLLOW-THROUGH AFTER A SUCCESSFUL STRIKE.
Conventions as in Fig. 35.

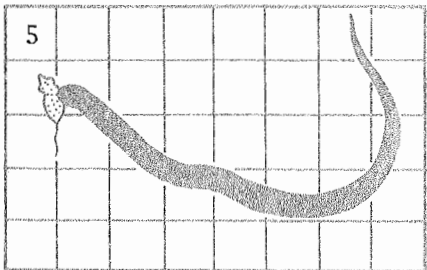
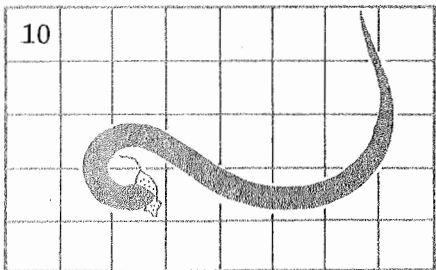
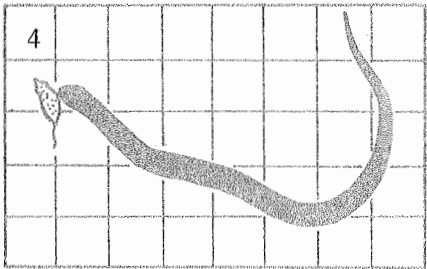
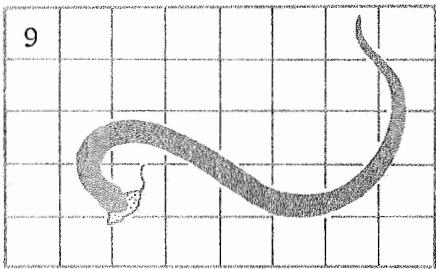
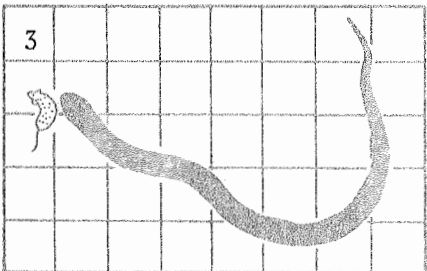
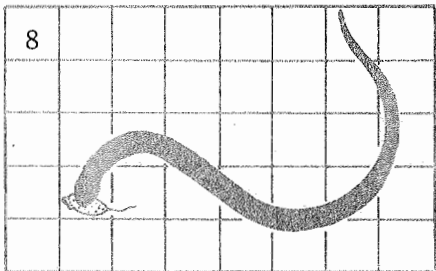
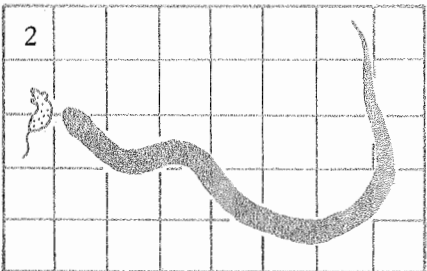
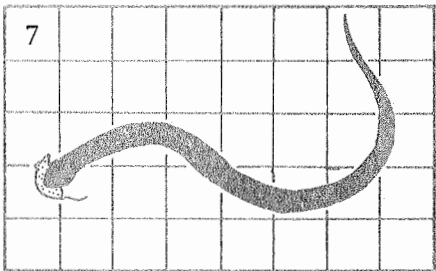
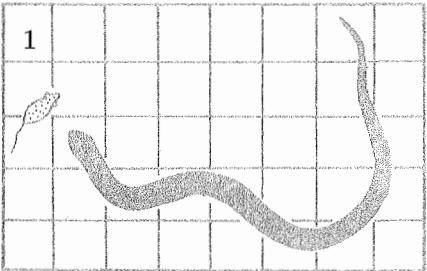
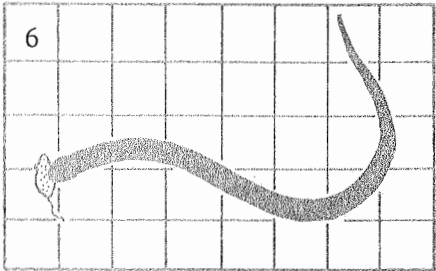


FIG.37 EXTREME COILING POSTURE EXHIBITED AS FOLLOW-THROUGH
OF STRIKE.
Conventions as given in Fig.35.

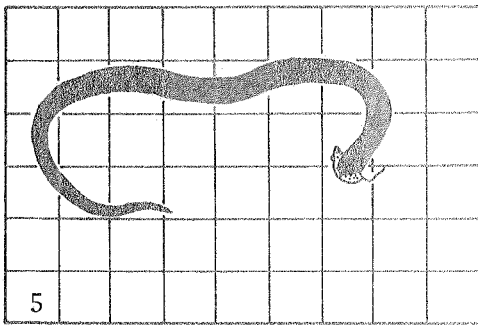
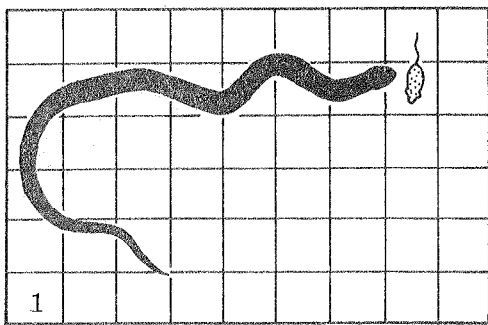
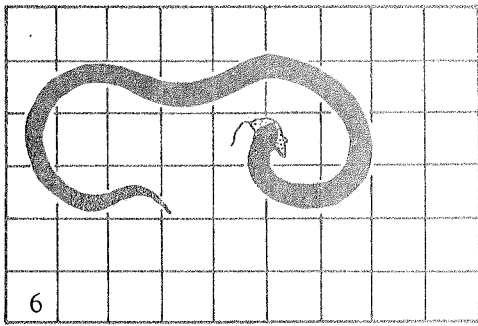
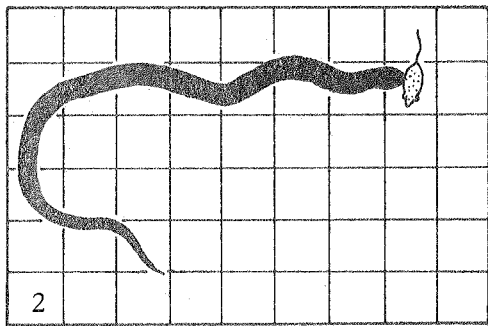
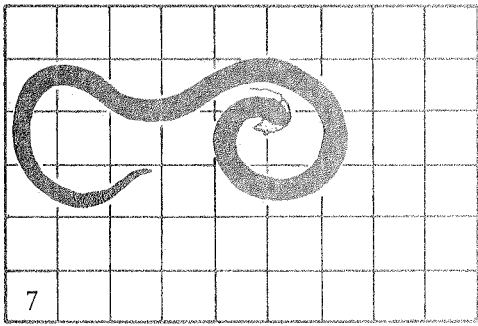
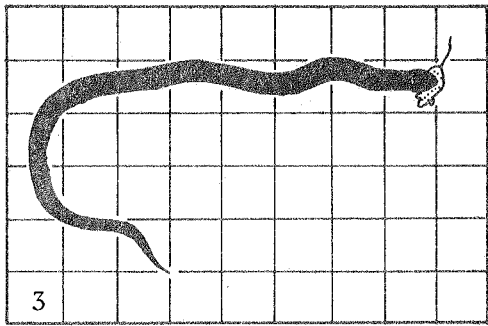
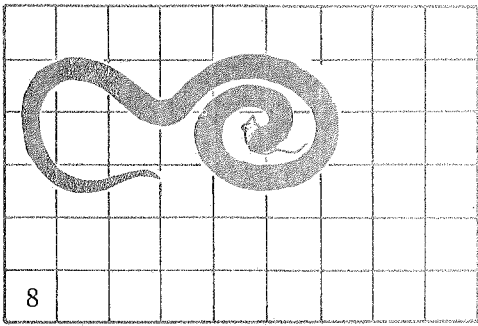
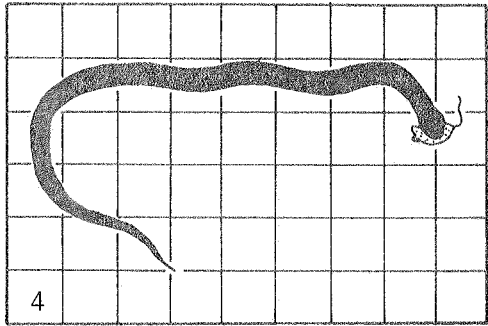
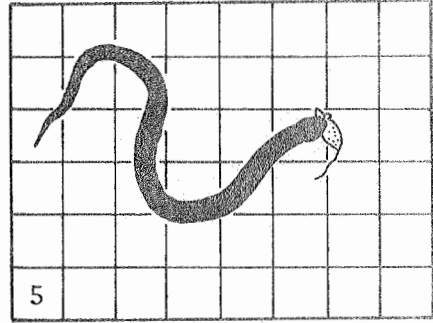
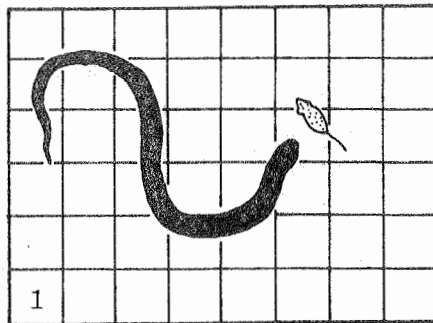
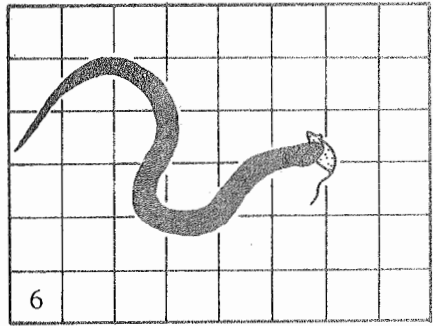
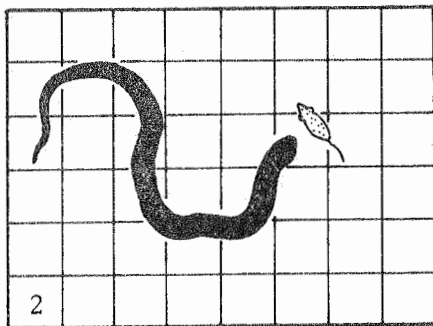
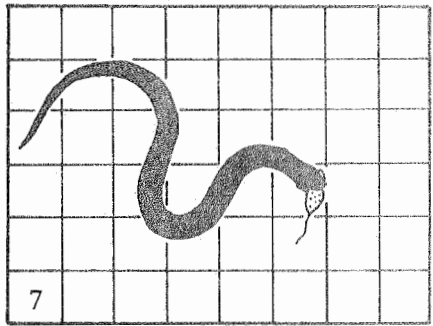
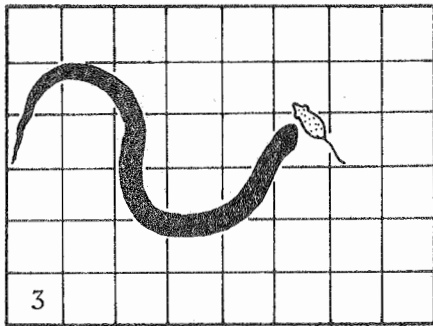
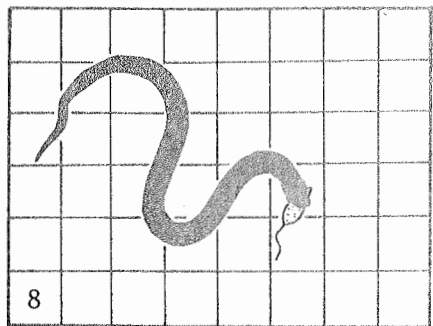
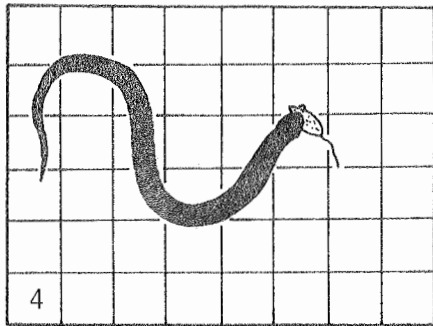


FIG.38 ROLLING ACTION (FRAMES 7 and 8) OF THE HOOKING TECHNIQUE EMPLOYED BY *N.A. HUMPHREYSI*.
Each frame represents a time lapse of 0.4s. Grids = 12.5cm and numbers represent frame sequence.



3.3.2c Time-relations of Prey-oriented Attack Behaviour

The mean velocity of striking estimated for *N.a. humphreysi* in the present study was 63.6 cm/sec, with a range of 40-100 cm/sec. recorded in twenty episodes of killing that were analysed in detail. Distances from which strikes were initiated (shown in Table 8), ranged from 1 cm to 5 cm averaging 2.24 cm. These estimates are based on the intervals between the onset (release) of the strike and the first contact with the prey. The time required for ensuing techniques varied considerably, depending on the precise strategy employed. In general, the forward-thrusting technique required 0.5 to one s to perform, whereas the duration of anterior hooking (as illustrated in Fig.36) was one to 1.5 s and that of complete lateral coiling (as shown in Fig.37) was variable, up to three s.

Durations of time taken for prey to die following envenomation by striking and biting are presented in Table 8. These data represent an average period of time (latency) to death, of 96.5 s, ranging between 10 and 257 seconds. The prey was considered dead when all visible signs of breathing and other movements finally ceased.

TABLE 8. PROTOCOL DATA FOR OBSERVATION RECORDED IN EXPERIMENT I.

Kill No.	Position of bite	Range of strike	Time for death(s)	Time for Ingestion(s)	Occurrence of hooking	Occurrence of dragging	Occurrence of release	Direction of Ingestion	
								head first	tail first
1	head	2 cm	80 sec	150 sec	x	x		x	
2	thoracic	5 cm	110 sec	180 sec	x	x	x	x	
3	thoracic	3 cm	90 sec	160 sec	x	x	x		x
4	head	1 cm	51 sec	180 sec	x	x	x		x
4a	thoracic	3 cm			x	x		x	
5	head	2 cm	64 sec	105 sec	x	x		x	
6	thoracic	1 cm	90 sec	105 sec	x	x	x		x
7	thoracic	2 cm	120 sec	145 sec	x	x		x	
8	thoracic	3 cm	10 sec	130 sec	x	x	x		x
9	lumbar	2.5 cm	38 sec	220 sec	x	x			x
10	pelvic	1.5 cm	40 sec	132 sec	x	x	x		x
11	head	2 cm	70 sec	135 sec	x	x	x	x	
12	pelvic	2 cm	85 sec	102 sec		x		x	
13	pelvic	2.5 cm	92 sec	118 sec	x	x			x
14	lumbar	2 cm	80 sec	159 sec	x	x		x	
15	head	3.5 cm	120 sec	168 sec	x	x		x	
16	head	2 cm	250 sec	133 sec	x	x	x	x	
16a	thoracic	2 cm			x	x		x	
17	lumbar	3 cm	156 sec	118 sec	x	x			x
18	head	2.5 cm	85 sec	125 sec	x	x		x	
19	thoracic	3 cm	70 sec	160 sec	x	x		x	
20	head	2 cm	80 sec	90 sec	x	x		x	
21	head	2.5 cm	80 sec	110 sec	x	x		x	
22	head	2 cm	58 sec	115 sec	x	x		x	
23	pelvic	1.5 cm	115 sec	158 sec	x	x			x
24	thoracic	1.5 cm	90 sec	160 sec	x	x		x	
25	lumbar	2 cm	102 sec	108 sec	x	x	x	x	
26	head	1 cm	57 sec	93 sec	x	x		x	
27	lumbar	2.5 cm	140 sec	125 sec	x	x	x	x	
28	thoracic	1.5 cm	115 sec	170 sec		x	x		x
29	pelvic	2 cm	98 sec	125 sec	x	x			x
30	head	1 cm	40 sec	80 sec	x	x		x	
31	thoracic	2.5 cm	45 sec	170 sec	x	x		x	
32	lumbar	2.5 cm	78 sec	190 sec	x	x	x		x
33	head	2 cm	91 sec	140 sec	x	x		x	
34	lumbar	3 cm	111 sec	172 sec	x	x			x
35	thoracic	1.5 cm	120 sec	168 sec	x	x		x	
36	thoracic	3 cm	160 sec	150 sec	x	x		x	
37	head	2.5 cm	40 sec	278 sec	x	x		x	
38	pelvic	2 cm	127 sec	191 sec	x	x	x	x	
38a	thoracic	4 cm			x	x	x	x	
38b	head	1 cm			x	x		x	
39	head	2 cm	257 sec	252 sec	x	x		x	
40	head	2 cm	65 sec	245 sec	x	x	x	x	
10a	thoracic	3 cm			x	x		x	

3.3.2d Releasing the Prey After Successful Striking Attempts

As the data in Table 8 indicate, fifteen of the total number of 45 incidents of striking recorded were followed by releasing the prey, representing a proportion of 33.3% of all episodes. The mouse usually contrived to be released and additionally, accomplished escape by struggling vigorously or actually biting the snake about the head and/or neck region. In most such instances, the snake then resumed the post-strike posture after releasing the mouse, and on four occasions it began active pursuit of the retreating prey.

After their release, mice often moved rapidly away from the snake until envenomation, from the bite began to exert its effects. Initially this consisted of the onset of muscular spasms, causing the limbs to stiffen, accompanied by erratic movements of the injured prey around the floor of the arena. When the prey had become relatively stationary on the floor of the arena, a variable number of convulsions (10-20) occurred before they eventually succumbed. The period of time (latency) between biting and death of the prey varied from 10-257 s.

In four instances, snakes were able to release another strike and capture the mice before death ensued. However, in the remaining eleven episodes, the mice had died before they had been re-located by the snakes. Snakes succeeded in locating decamping prey by following essentially the same route that the mice had pursued in the course of their escape. For example, on one occasion, when a mouse had fled, it moved around the perimeter of the arena away from the snake (consequently out of sight of the snake) and died in the centre of the arena, the snake did not approach the carcass of the prey by the most direct route but followed its trail until it located the mouse. Nevertheless, in five of the eleven instances, when the death of the prey occurred before it was re-located, the snake was within visual range of the mouse as it died and subsequently moved directly toward it. Detection of the prey by the snake was characterised by the orientation of its head towards the mouse during its post-release behaviour.

3.3.2e Analysis of the Orientation of Biting

For the purpose of analysing the specific orientation of biting, in relation to the body of the prey, the latter was arbitrarily divided into four principal regions. These are shown in Fig.39 and are as follows: i) head, ii) thoracic, iii) lumbar and, iv) pelvic areas. Table 9 shows the data obtained for estimated striking distances and the duration of time to the death of the prey, in relation to specific areas bitten. Seventeen bites were delivered to the head region, representing 37.8% of the total number of bites recorded. Fifteen (33.3%) were directed at the thorax, six (13.3%) at the lumbar area, and seven (15.6%) at the pelvic region. Compared with an expected frequency of 11.3 bites at each area, chi-squared analysis gave a value of 8.24 ($df=3$), $P>0.05$ suggesting that the orientation of bites in various areas of the body does not occur at random.

Mean distances and standard errors of striking estimated for each of the areas bitten are shown in Fig.40. These data indicate that the shortest mean strike distance was recorded when the prey received bites to the head area, and the pelvic, lumbar and thoracic areas, respectively, received bites from increasing distances, in that order. Two-sample 't'-tests (unpaired) were applied to each combination of bite areas possible to determine any significant variation or preference within the sites of biting. The results of these tests (head-thoracic: 't' = -5.4, $df=30.0$; head-lumbar: 't' = -5.1, $df=21.0$; head-pelvic: 't' = -4.0, $df=22.0$; thoracic-lumbar: 't' = -1.8, $df=19.0$; thoracic-pelvic: 't' = -1.1, $df=20.0$ and lumbar-pelvic: 't' = -2.5, $df=11.0$) demonstrate that comparisons between thoracic-lumbar and thoracic-pelvic areas did not yield significant differences, whereas comparisons between the head-lumbar, head-pelvic and lumbar-pelvic regions disclosed significant differences in the orientation of biting.

Fig.41a is based on the relationship between time (latency) to death of the prey and the part of the body bitten, represented by means and standard deviations estimated for specific localities. These data illustrate that prey bitten in the pelvic area died after a longer period of time than those that received bites in the other three areas of the body (latencies to death between these were

FIG. 39 POSITION ON THE BODY OF THE MOUSE WHERE BITES OCCURRED DURING EXPERIMENT I.

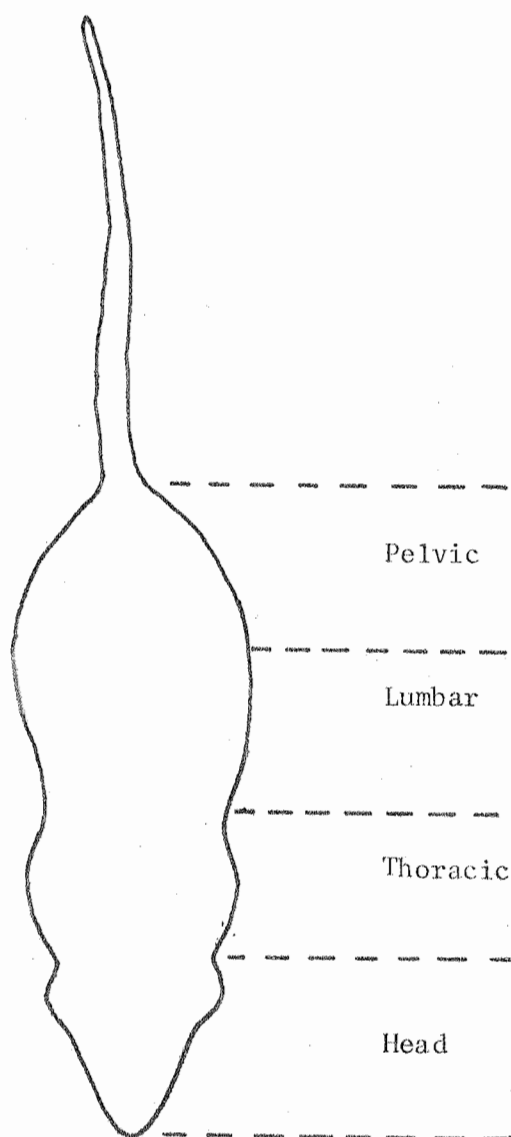
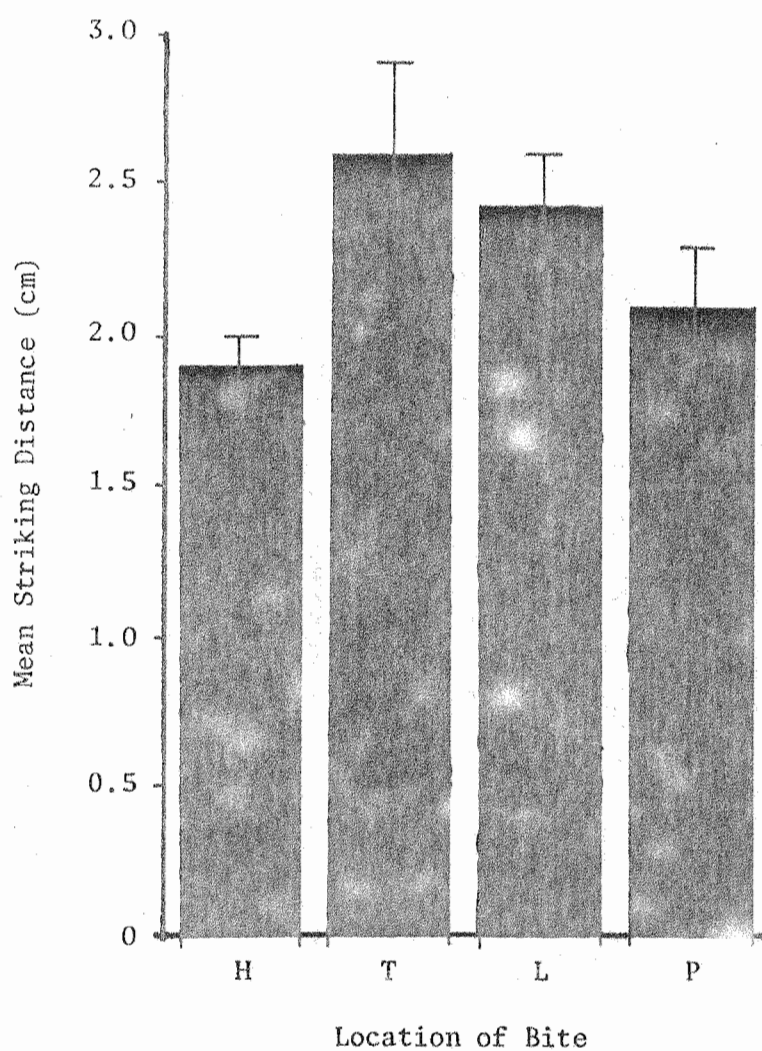


TABLE 9 STRIKING DISTANCES AND INGESTION TIME IN RELATION TO SPECIFIC BITE AREAS.

Head		Thoracic		Lumbar		Pelvic	
strike distance (cm)	ingestion time (s)	strike distance (cm)	ingestion time (s)	strike distance (cm)	ingestion time (s)	strike distance (cm)	ingestion time (s)
2	80	5	110	2.5	38	1.5	40
1	51	3	90	2	80	2	85
2	64	3		2	102	2.5	92
2	70	1	90	2.5	140	3	156
3.5	120	2	120	2.5	78	1.5	115
2	250	3	10	3	111	2	98
2.5	85	2				2	227
2	80	3	70				
2.5	80	1.5	90				
2	50	1.5	115				
1	57	2.5	45				
1	40	1.5	120				
2	91	3	160				
2.5	40	4					
1		3					
2	257						
2	65						

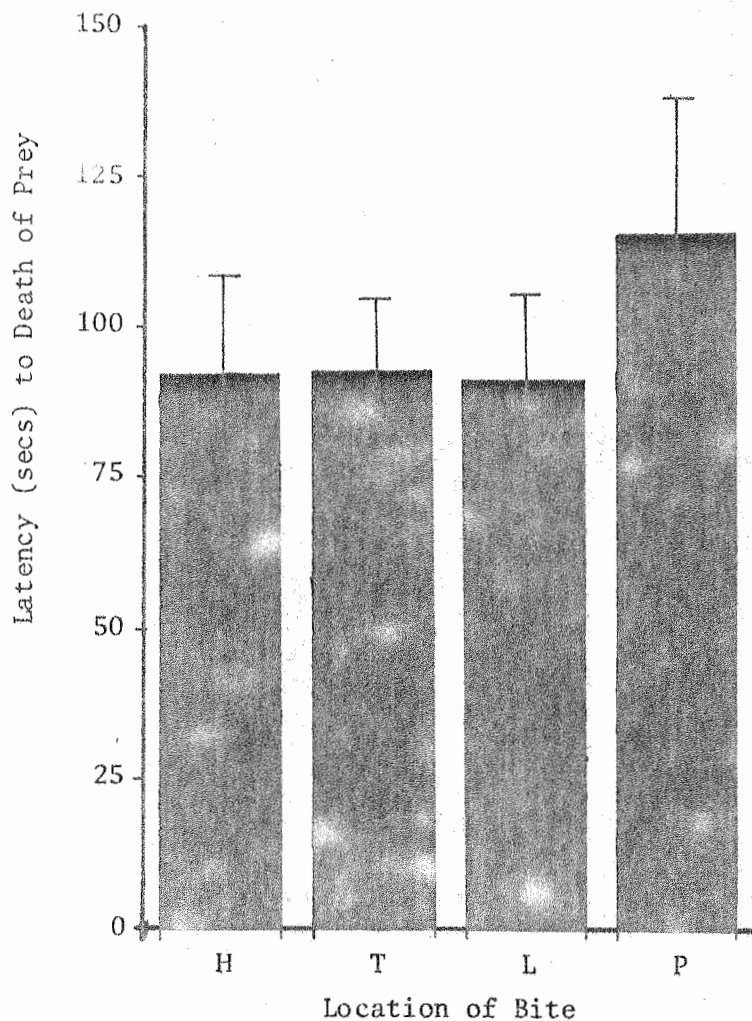
FIG.40 STRIKING DISTANCES IN RELATION TO LOCATION OF BITES.



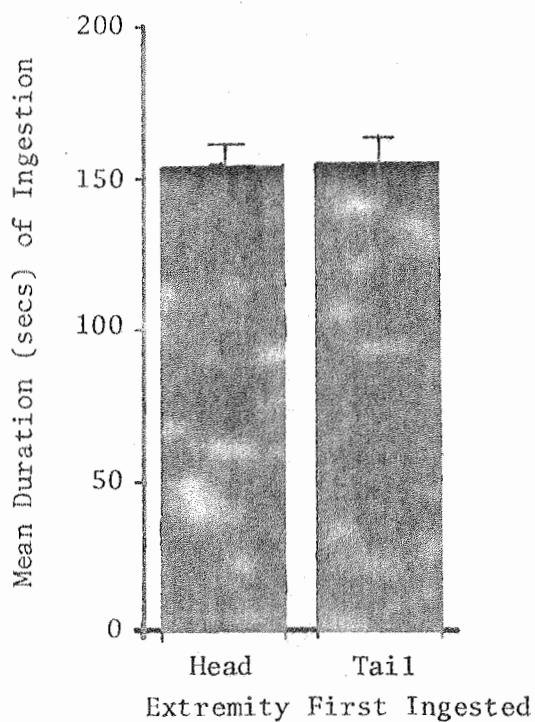
H = Head
T = Thorax
L = Lumbar
P = Pelvis

FIG. 41

LATENCY TO DEATH OF PREY AND DURATION OF INGESTION IN
RELATION TO ORIENTATION OF KILL AND FEEDING RESPONSES.



(a) Latency to Death of Prey in Relation to Location of Bite.
(Conventions as in Fig. 30).



(b) Duration of Ingestion in Relation to the Initial
Orientation of Feeding Response.

similar). Analysis (two-sample 't' tests) between paired combinations of the areas bitten showed that there was no significant variation among the various regions with respect to the latency of death of the prey (head-thoracic: 't' = -0.1, df = 25.0; head-lumbar: 't' = 0.0, df = 20.0; head-pelvic: 't' = -0.8, df = 21.0; thoracic-lumbar: 't' = 0.0, df = 15.0; thoracic-pelvic: 't' = -1.0, df = 16.0; and lumbar-pelvic: 't' = -0.9, df = 11.0).

3.3.2f Ingestive Behaviour

After the demise of the prey, snakes generally began to manoeuvre the carcass to a suitable position, presumably to facilitate ingestion. In most instances when the definitive bite was directed at the lumbar or pelvic area of the body of the prey, the snake manoeuvred its mandibles and upper jaw across the carcass without entirely releasing it. The jaws were used to grasp the posterior region of the body and ingestion began in this area. Similar techniques were employed when the prey had been bitten on the head or thoracic area. In these situations, snakes invariably manoeuvred toward the anterior extremities of the mice and the prey was ingested head-first.

During preliminary processing of prey, the snakes exhibited characteristic types of behaviour. These consisted of backward dragging actions over the floor of the enclosure. As Fig.42 demonstrates, the snakes moved the anterior part of their bodies in a reverse motion (away from the site of initial prey-capture) while moving the posterior of the body forward. The example given in Fig.42 is representative of that observed on all occasions; this type of behaviour was highly stereotyped and characteristic of all episodes of successful prey-capture. Positioning and subsequent ingestion of the prey were constantly accompanied by these dragging actions for the entire duration of their performance. The distance of dragging ranged from 10 to 50 cm. Fig.43 illustrates a less intense form of dragging than that in Fig.42. The manoeuvring and ingestive techniques exhibited by all of the snakes observed also followed a distinctive pattern. This process consisted of "walking" the head, and feeding apparatus, over the body of the prey, thereby drawing the carcass into the mouth. During the jaw-walking activity one of the sides of both the upper and lower jaws were alternately released of their grip on the prey. Each movement was associated with one side of the head of the snake whenever a given side of the jaw was released. The released side of both the upper and lower jaw, was subsequently manoeuvred forward over the body of the prey, anchored into the carcass and then withdrawn to its normal position, thereby drawing the prey into the snake's mouth. The process was then repeated on the other side of the jaw.

The above sequence of ingestive events is illustrated in Fig.44,

FIG.42 BACKWARD DRAGGING TECHNIQUE EMPLOYED BY ALL SUBJECTS EXAMINED.

Each frame represents a time interval of 20s, numbers indicate frame sequence. Each grid equals 12.5cm.

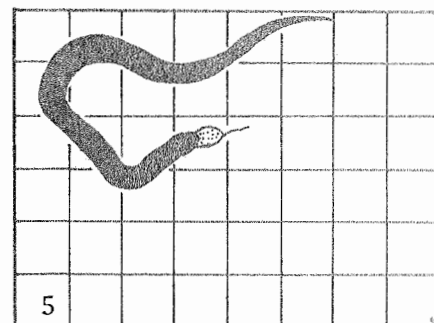
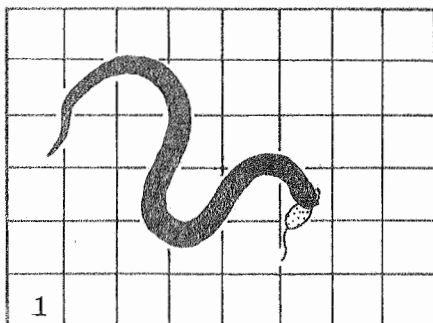
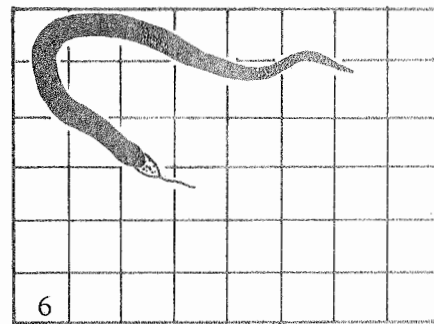
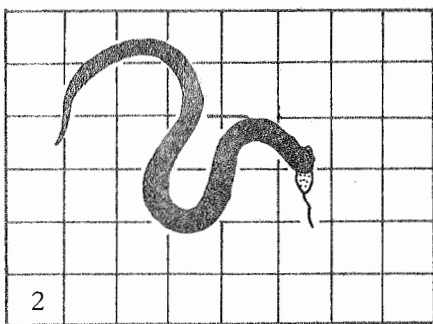
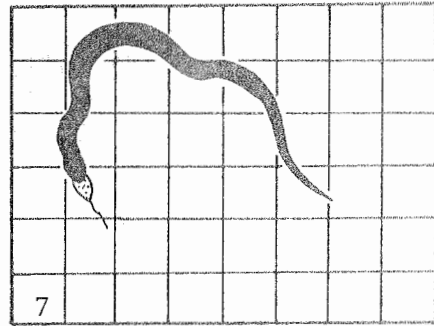
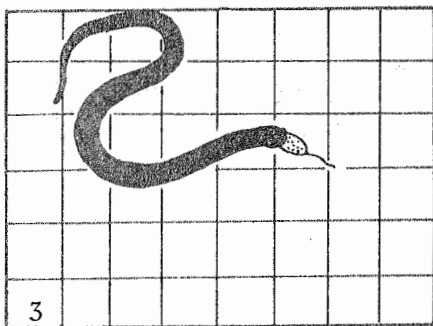
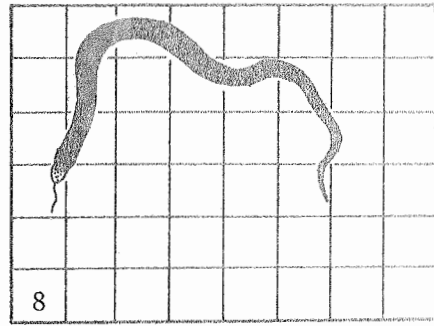
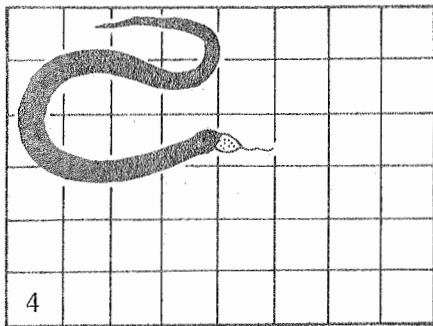


FIG.43 A LESS INTENSE FORM OF BACKWARD-DRAGGING EXHIBITED BY *N.A. HUMPHREYSI* IN THE OPEN ARENA.
Each frame represents a time lapse of fifteen s.



and the five components given may be described as follows:

a) starting position, with the right side of the upper and lower jaws having released their grip on the body of the prey.

b) manouvering forward of the right side of the upper and lower jaw and anchoring the fang and associated teeth into the carcase.

c) the right side of the jaw mechanism is withdrawn, drawing the prey into the mouth. At this stage the left side of the jaw mechanism is released from its grip on the body of the prey.

d) the left side of the jaw mechanism is manouvered forward over the carcase and the teeth are anchored into the body.

e) the left side of the jaw mechanism is withdrawn to its normal position, drawing the prey further into the mouth of the snake. At this point, the right side of the upper and lower jaw mechanism is released from its grip on the carcase and the cycle resumes as it began in a).

Mean ingestion time, as given in Table 8, was 151.1 s, with a range of 80-278 s.

Of the 40 sequences of ingestion recorded, 27 were oriented to the anterior part of the body whereas thirteen were directed at posterior regions. A chi-squared figure of 4.9 ($df=1$) gives the result $P > 0.05$, suggesting that the difference in the orientation of ingestion was significant. When the positions of biting are examined in relation to the orientation of the ingestive process, the results show that 71.1% of prey were bitten in the anterior or head and thoracic area of the body and 28.9% were bitten in the posterior of the body or the lumbar and pelvic region. These results appear to accord well with the observation that 67.5% of the prey were ingested from the anterior end and 32.5% were ingested from the posterior end. The slight discrepancies between the relative proportions may be the result of consuming prey after re-locating it, rather than directly after biting and not necessarily ingesting them at, or near the bitten area.

A comparison of the mean duration of ingestion estimated for anteriorly- and posteriorly-oriented ingestive actions is given in

FIG.44 THE SEQUENCE OF INGESTIVE COMPONENTS EXHIBITED BY *N.A. HUMPHREYSI*, USING MICE AS A PREY-SPECIES (actual size).

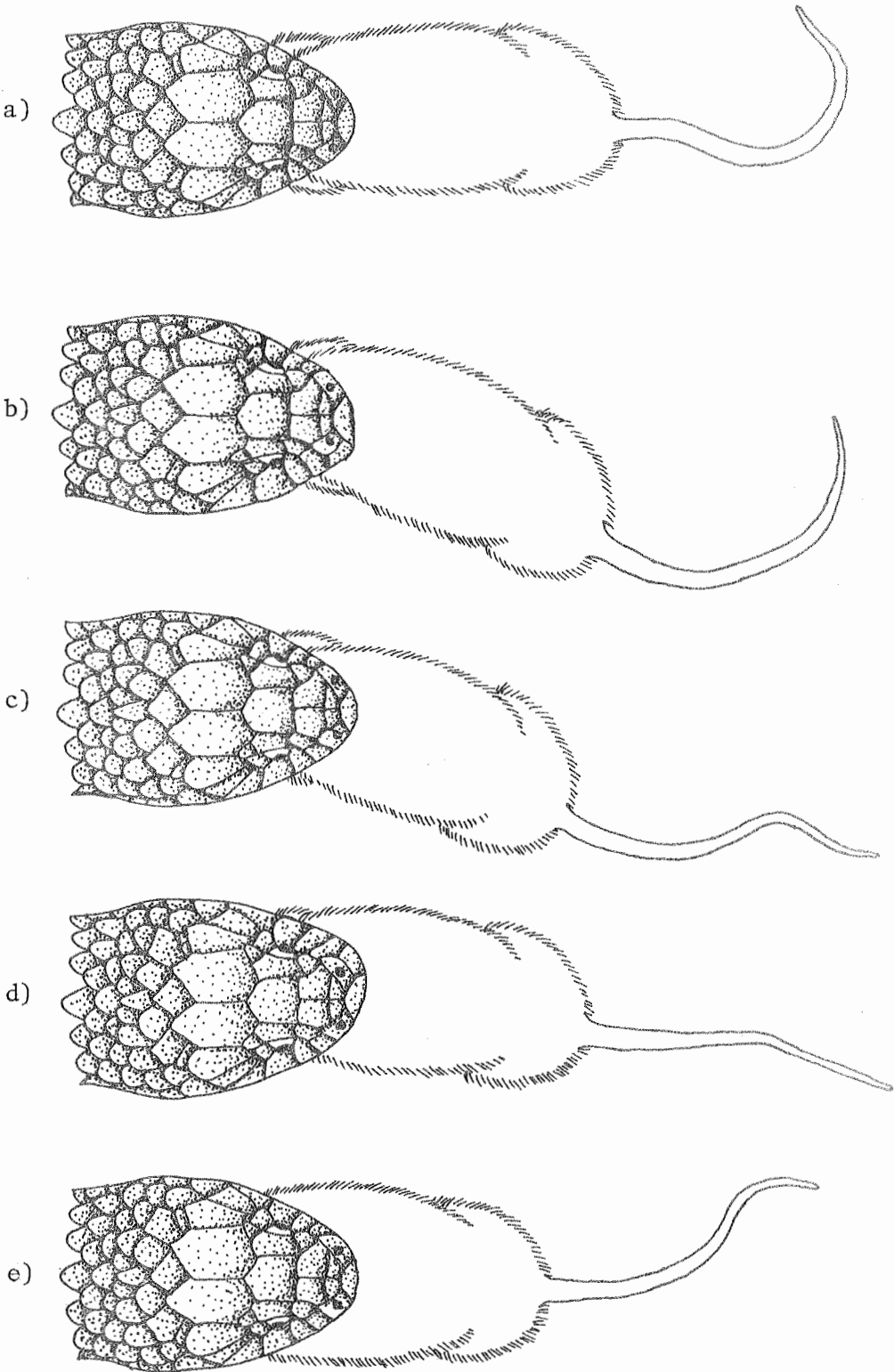


Fig.41b. As the average values and standard errors indicate, the variation between the two types of response is negligible; indeed, the results of a 't' test (unpaired) yielded a value of -0.2 (df = 38) therefore showing the variation between individual times for each ingestive direction to be non-significant.

3.3.2g Post-ingestive Behaviour

Following the ingestion of prey, snakes generally immediately began to perform "yawning" actions as mentioned in Section 2.2. This type of behaviour consisted of gaping, or opening the mouth, and disfiguring the jaw mechanism, particularly the lower mandible. The yawning actions were similar in form to the distortions of the jaws described for ingestive behaviour in Section 3.3.2f. The duration of individual yawning did not exceed eight s on any occasion and a series of yawning motions lasted no longer than two min.

When a yawning-sequence had been concluded, the snakes usually began moving the anterior part of the body laterally, from side to side, in a slow arc while carrying out tongue-flicking actions. The post-ingestive tongue-flicking actions were a combination of the prolonged and repeated types previously described. After a period of time varying from one to two min the snakes usually began to move the entire body around the arena, while continuing to practise prolonged tongue-flicking. In ten of the episodes recorded the snakes assumed a coiled or looped posture within five minutes of completely ingesting the prey. In other episodes the snakes were actively carrying out investigatory behaviour around the arena at the duration of five min.

3.3.2h Frogs and Lizards as Prey in Open Conditions

The experimental procedures employed in a series of observation trials, designed to test responses to poikilothermous prey, were similar to those used in the study testing predation on mice. Since the frog *Litoria ewingi* constituted the major proportion of alimentary canal content (Section 2.3) and the small skink *Leiolopisma metalicus* was the most abundant skink in the study area (Section 2.3), it was considered appropriate to use these animals in this series of observations. A total of twenty trials were carried out, each individual snake being tested for responses to each of the selected prey-species. During all trials the temperature of the arena was constantly maintained at 20C⁰ and each snake was permitted a twenty minute acclimation period before the prospective prey was introduced into the arena.

Searching and approach-behaviour of the snakes closely resembled those described in Section 3.3.2a. However, active forms of approach were only exhibited on five occasions when frogs were being used as prey, and not at all when lizards constituted the potential prey. No attempts at striking and no incidents of successful killing were recorded in any of the twenty trials testing ten snakes. In trials using lizards as the prospective prey species, the snakes appeared to be incapable of approaching closer than 25 cm before lizards moved away. This type of alternating approach and withdrawal between snakes and lizards continued for two h in one trial before the snake coiled up under the light bulb in the corner of the arena.

On the occasions when frogs were used as potential prey, three major types of behavioural sequences were observed, namely: i) the frog leaped away before a snake approached to a distance of less than 25 cm, ii) the snake approached to a distance of less than ten cm, adopting a pre-strike posture but the frog jumped away before the strike was released (this occurred in four instances) or, iii) the frog remained motionless, with its body flattened in contact with the substrate, on the floor of the arena, or at the junction of the walls and the floor, and remained immobile while the snake approached. In two out of the ten episodes examined in detail, snakes literally moved directly over the frogs without evidencing any sign of having

noticed them. In four trials, snakes approached to within five cm of frogs lying flat on the floor of the arena and showed no indication of recognising them as potential prey.

In order to test the possible effect of the prey-killing and feeding-motivation of the snakes used in these experiments, a single mouse was introduced to each snake in the arena immediately after the frogs or lizards had been removed. The mice were killed and ingested on each of these occasions.

3.4 EXPERIMENTAL SERIES II : INVESTIGATION OF PRE-CAPTURE WITHIN AN ARTIFICIAL BURROW

3.4.1 Introduction

During the course of field-observations and trials and analyses carried out in Experimental Series I, several of characteristic behavioural patterns emerged which indicated that *N.a. humphreysi* may feed on small animals while they are within their burrows. The characteristics or factors leading to this hypothesis are:

- a) foraging activities in a natural situation apparently involved searching around the perimeter, of obstacles, at ground-level,
- b) the prey species found in alimentary canal analysis were found to inhabit burrows beneath rocks and fallen timber, c) the snakes appeared to be unable to capture "natural" prey in an open-field situation, d) striking was highly inaccurate over distances greater than five cm, e) hooking of the anterior part of the body may be an adaptation to pinning the prey to the burrow wall, as may be arching of the body, f) backward-dragging may be an adaptation to drawing the prey clear of the burrow entrance prior to, or during, ingestion.

These behavioural characteristics led to the design and employment of the apparatus used in Experimental Series I and II.

3.4.2 Materials and Methods

Before the commencement of experimental trials, each snake was individually tested to ascertain whether it was capable of feeding in complete darkness or not. The relevant procedure consisted of introducing a mouse into the home-cage of each snake shortly after 1800 h, when the light source had ceased to operate. The roof of each home-cage was then completely covered with a hessian sack to further exclude incident light. Each cage was subsequently examined (before sunrise) to ascertain the outcome of the encounter. The results of these observations showed that within a period of three days, all snakes had succeeded in killing prey in complete darkness.

The apparatus used in this series of in-burrow killing experiments consisted of a Perspex box with a three cm square entrance and a transparent roof. This was placed in a corner of the arena and the two exposed sides were covered by a wooden frame. The roof of the box was covered by a black plastic funnel-like structure extending to the roof of the arena; through the opening of this, in-burrow prey-killing techniques were observed. In the course of this series of tests, mice were individually introduced to the box-structure burrow, together with a small quantity of litter from mouse home-cages, contaminated with urine and faeces. Food was also provided for the mice. These measures ensured that mice remained inside the burrow for the duration of testing. When the prospective prey was in the burrow a snake was introduced to the centre of the arena and observation commenced.

The funnel was sealed while the snake moved around the arena, but when it approached the burrow-apparatus, the mouth of the funnel was opened sufficiently wide to permit the observer to record in-burrow activity. In some instances, the sequence of events was filmed from directly above the roof of the arena.

3.4.3 Results

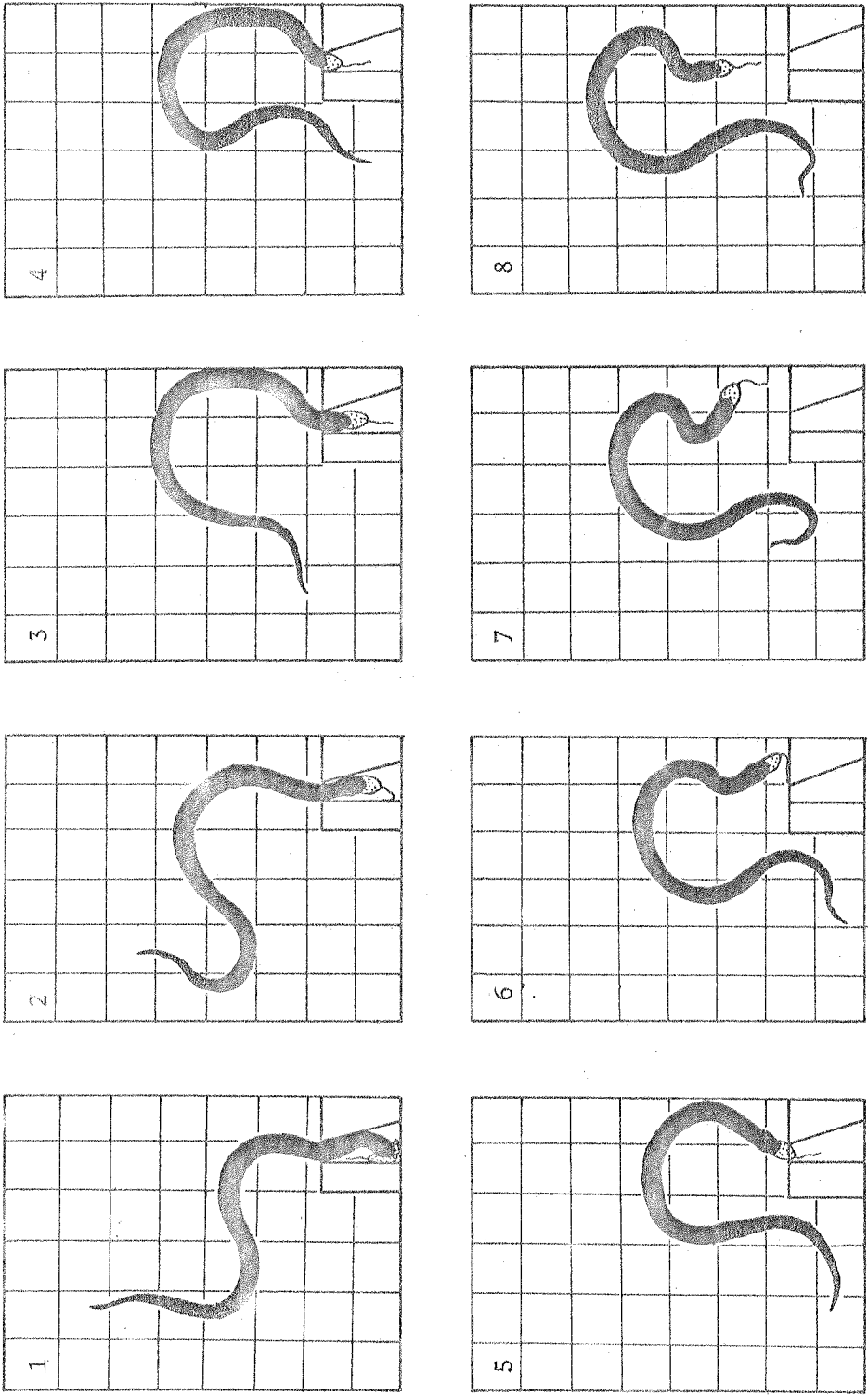
The following description is a generalised interpretation taken from eight in-burrow kill occasions. As snakes moved around the arena, "prolonged" tongue-flicking was a conspicuous activity. However, when they approached close to the burrow entrance, frequencies of tongue-flicking increased and these were of the "repeated" type. The snakes usually probed around the perimeter of the wooden frame, surrounding the artificial burrow, until they located the entrance of the burrow. As they entered the burrow, the contours of the snakes obliterated almost all of the illumination in the burrow proper. The snakes then approached the mice which generally retreated to the rear of the burrow, and released a short strike, thrusting forward from a distance not exceeding five cm.

In the ensuing action, the anterior part of the body of the snake "hooked" laterally and "arched" in a manner that forced the body of the mouse onto the floor of the burrow. In this position, the snake held the mouse against one side of the burrow while procuring leverage of its body against the opposite side, further buttressed by pressure against the ceiling of the burrow. Fig.45 shows this position (frame 1), as well as the backward-dragging sequence of actions, following the death of the prey.

The hooking-position was maintained by the snake while forcing the mouse against the wall of the burrow by lateral and downward pressure, until the prey had died. Thereafter, the snake began the characteristic backward-dragging movements of the anterior part of the body while the posterior part was moved in a forward direction. As Fig.45 shows, these movements continued until the mouse had been dragged clear of the burrow-entrance. The performance of dragging movements was not constant but intermittent, in that snakes periodically interrupted this activity and manipulated mice further into their mouths as previously described (Section 3.3.2f), for brief periods before resuming the dragging movements. In no recorded instance did the total amount of time required to withdraw a mouse from the burrow exceed ten minutes.

Ingestion of the mouse was accomplished as described in Section 3.3.2f. Durations of the process were not recorded in this series

FIG. 45 PREY-RESTRAINT AND BACKWARD-DRAGGING TECHNIQUES OBSERVED IN EXPERIMENTAL SERIES II.
Each frame represents a time lapse of fifteen seconds.



of experiments because of the difficulty of conducting detailed in-burrow observations in conditions of partial darkness and the arduous task of operating video-equipment while backward-dragging occurred. Following ingestion, the snakes behaved similarly to those described in Section 3.3.2g (e.g. performing investigatory head movements and other actions). In six of the eight trials completed, the snakes returned to, and re-entered the burrow. In the remaining two tests, the snakes adopted a tightly coiled position in a corner of the arena near the light-source. The individuals that re-entered the burrow probed near the walls of the burrow and performed repeated tongue-flicking activities for one to five min before withdrawing to below the light-source, adopting a coiled position.

3.5 EXPERIMENTAL SERIES III : NATURALISTIC INVESTIGATIONS OF IN-BURROW PREY-KILLING BEHAVIOUR

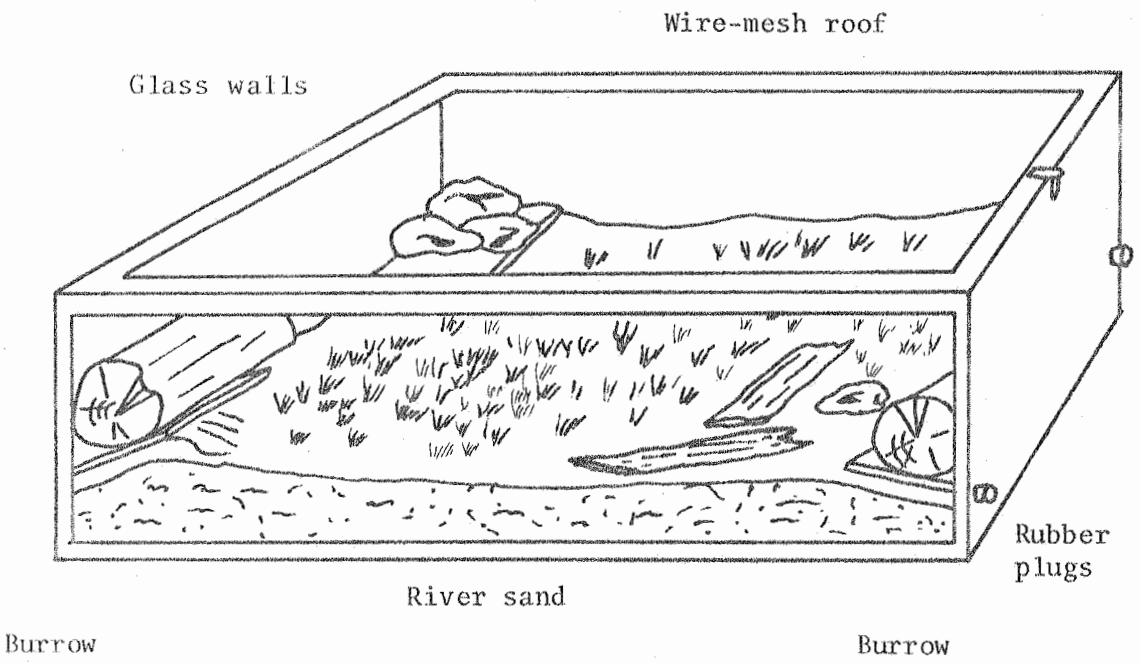
3.5.1 Materials and Methods

For the purpose of naturalistic observations on predatory behaviour, an enclosure was constructed. This consisted of two glass walls, two wooden walls and a door opening on the roof, composed of fly-wire mesh (Fig.46). The floor of the arena was covered with a layer of coarse river-sand and dolerite, podsollic soil to a depth of ten cm and a further covering of grass and leaf-litter. A burrow was constructed at either end of each glass wall by excavating in the mixture of sand and soil and providing a sheet of bark to represent the roof of the burrow (Fig.46). The roof was weighted down by small logs placed over the burrows at one glass wall and rocks placed over the two burrows at the other glass wall. A three cm hole was drilled through the wooden wall, at the rear of each of the four burrows; these were closed by means of rubber stoppers.

Heat was provided by a double strip heater positioned directly above the roof of the arena. Light was provided by a single 100-watt light-bulb suspended over the roof of the arena, at a height of 30 cm. During observations, the glass walls were covered with thick, black plastic sheeting, leaving only the rear half of the burrow exposed to light. This permitted observations of activity within the burrow, from the side, apparently without being noticed by the subjects.

The initial procedure consisted of introducing a snake into the arena, simultaneously rendering the lighting and heating equipment operational. When the snake became active and exhibited movement of the type observed in the wild (described in Section 2.2), two frogs (*Litoria ewingi*) were introduced into the rear of each of the four burrows by removing the rubber stoppers. The latter were replaced after the frogs were released, in the burrow, to prevent their escape. The activity of the snakes in the arena was observed from a distance of 50 cm above the roof of the arena until they entered one of the burrows; thereafter observations were made through the lateral glass wall.

FIG.46 OBSERVATION ARENA USED IN EXPERIMENT III.



3.5.2 Results

The results described here are a general description from fifteen in-burrow, prey-capture episodes which occurred over a period of ten trials (one trial with each individual snake). Five of the subjects killed within the burrow, on two occasions during their trials.

The nature of this series of observations demanded that the laboratory be maintained in darkness, with the exception of the lighting and heating equipment used within the enclosure. As a consequence, the use of cinematography and still photography was not possible due to the possibility of distracting the animals by prolonged, or flashes of light created by photographic equipment while they were active in the burrows. Illustrations were accordingly made, as pencil sketches of the in-burrow activities, prepared during observations in semi-darkness and these were subsequently modified, by using live subjects in bright illumination, to produce more realistic visual records.

Each of the snakes observed was placed in the centre of the enclosure before the external light-sources were extinguished and the enclosure-lighting and heating switched on. The range of temperatures in the home-cages of the snakes was 10-14C⁰ at the time when the animals were removed for testing. In the conditions of the arena, snakes invariably assumed a tightly-coiled posture (described in Section 2.1) within five minutes after being placed onto the floor of the enclosure. When the temperature of the enclosure reached 25-28C⁰ (measured by a thermometer on the floor of the enclosure) the snakes generally adopted the pre-foraging, looped posture previously mentioned. These events usually occurred within a period of one h after introduction into the enclosure. The temperature of the enclosure was maintained at 28C⁰ for the remainder of the observation period.

After an initial basking-period not exceeding 30 min, the snakes usually moved around the enclosure engaging in prolonged tongue-flicking (described in Section 3.3.2a) and probing the perimeter of the obstacles (bark, rocks and logs) on the floor of the enclosure. This activity is described more fully in Section 2.2. Because of

the size of the enclosure, the snake did not "forage" for more than ten min before they located one of the four burrow-entrances.

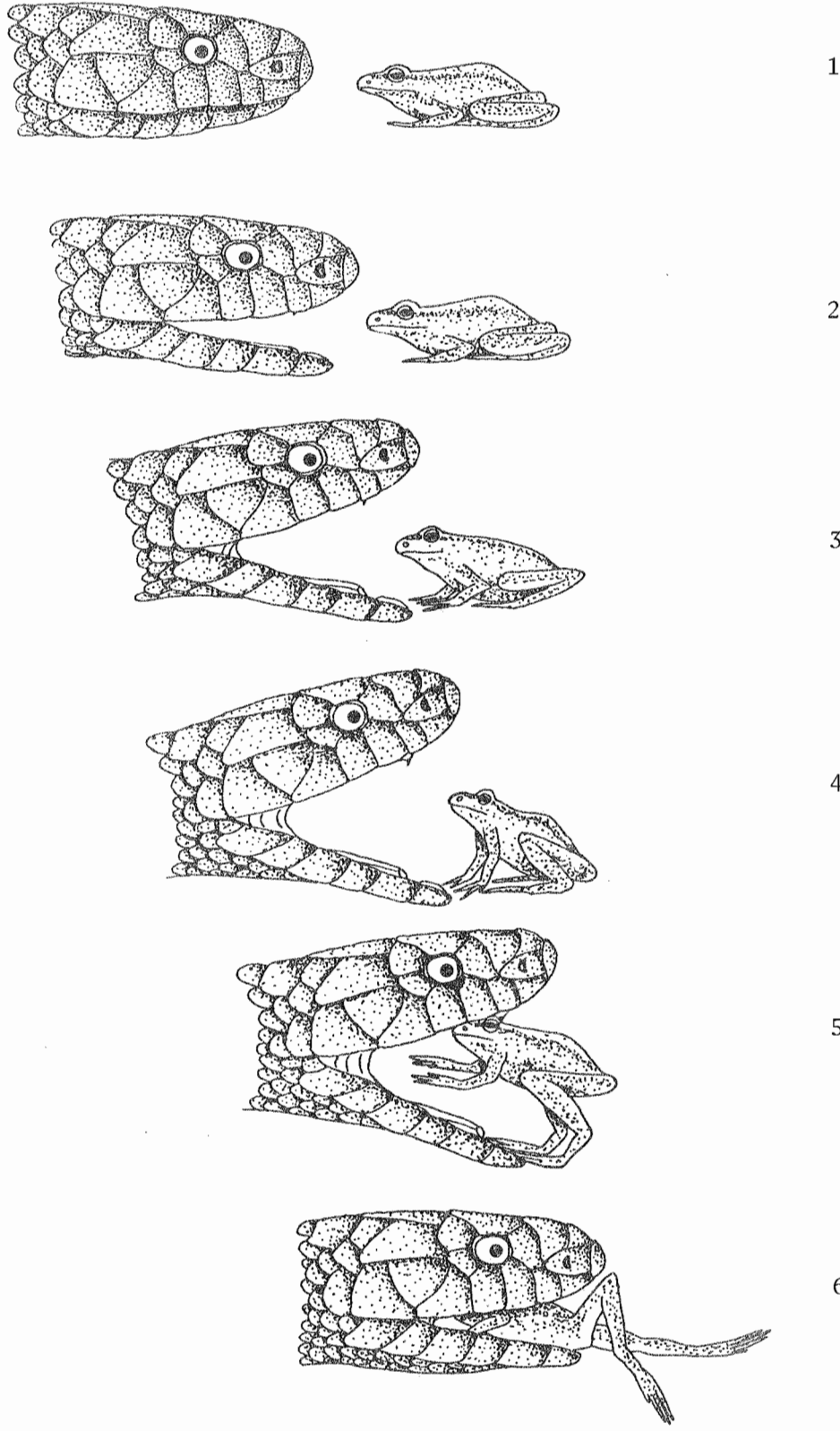
3.5.2a Activity Within the Burrow

After entering the burrow, frequencies of tongue-flicking by the snakes usually increased to constitute the "repeated" type of tongue-flicking described in Section 3.3.2a. Almost all of the light impinging on the burrow was occluded by the snake as it entered. The frogs remained in a crouched posture on the floor of the burrow as the snake approached (Fig.47). In the course of the fifteen episodes of killing observed, two distinctive forms of prey-capture behaviour were noted. One of these was accomplished by rapid striking, the second was by a slower, "engulfing" method.

The rapid striking technique of capture employed within the burrow was similar to that in the strikes used by snakes in the Experimental Series I and II. However, in the current series of experiments, only limited space was available for increasing the amplitude of the sinusoidal curves of the anterior part of the body prior to delivering strikes. The snakes nevertheless increased the amplitude of their anterior curves as much as this appeared feasible within the confines of the burrow; they further increased those of curves of the body situated immediately outside the burrow. Precise distances of striking were not estimated for the six rapid strikes performed by three snakes, but it was noted that these did not exceed five cm. They generally ranged between 1 and 3 cm. The characteristic behavioural elements of hooking, arching and backward dragging were observed on all (six) occasions when rapid striking occurred.

The nine incidents of slow "engulfing" prey-capture techniques observed in seven snakes, were all similar in expression. These methods consisted of a number of distinctive actions: Firstly, the snake approached the prey to within one and two cm of the frog, while engaging in tongue-flicking (the tip of the tongue appeared to establish actual physical contact with the prey); secondly, the snake usually opened its mouth in a wide gape as it gradually moved in the direction of the prey; thirdly, the snake generally moved forward and enveloped the prey in its open mouth and finally, the snake closed its mouth, thereby completing the process of capture. During this sequence of events, the prey showed few indications of overt escape-behaviour until envelopment occurred. At this stage

FIG.47 SLOW PREY-ENGULFING TECHNIQUE EXHIBITED BY SUBJECTS PERFORMING PREY-CAPTURE WITHIN A NATURALISTIC BURROW. Numbers represent sequence of events; the entire sequence being no longer than three seconds.



it usually attempted to leap away. The time required for completion of the slow engulfing technique, described above, was two to five s. Fig.47 illustrates a typical in-burrow sequence of this type of in-burrow prey-capture. Following the procurement of the prey, the snakes exhibited hooking, arching and dragging as previously described in rapid-strike killing episodes.

During this series of prey-capture trials it was noticed that the frogs were still alive and constantly struggling while being ingested by the snake. This greatly contrasts with earlier experiences when laboratory mice were invariably observed to be dead before they were ingested.

3.6 DISCUSSION

3.6.1 Experimental Series I

Although the snakes were placed in an open-field arena, which was markedly different from the terrain characteristic of their natural habitat, they exhibited several distinctive forms of behaviour which were considered analogous to the typical behavioural events observed in the field. The first category of these to be recorded was searching behaviour. This consisted of a series of probing movements performed while the snake moved around the interface of the wall and floor in the arena and were generally similar to the muzzling activities described during the field observations. In conjunction with this behaviour, the snakes performed tongue flicks of a type similar to those observed under natural conditions. The second category of behaviour exhibited within the arena, also paralleling those observed in the field, was the basking behaviours. The posturing performed by the subjects under the light-source was similar in expression to corresponding forms of behaviour observed in the field.

The observed increase in the frequency of tongue-flicking, accompanying the recognition of prey within the arena recorded in the present study of *N.a. humphreysi* has also been previously recognised in investigations of the eastern king snake *Lampropeltis getulus* (Williams and Brisbin, 1978) the cottonmouth snake *Agkistrodon piscivorus* (Kardong, 1975) and the common garter snake *Thamnophis sirtalis* (Burghardt, 1969). The authors of these studies were able to deduce that the increase in the frequency of tongue-flicking shown by the subjects of their respective surveys were responses indicating anticipation of prey-capture. The function of the increased frequency of tongue-flicking was considered to be the transfer of increasing amounts of specific substances (chemical stimuli) to the vomeronasal nerve, via the organ of Jacobson, thereby permitting accurate prey-recognition. In a series of experiments using artificial lesions on adult garter snakes Halpern and Frumin (1979) were able to show that feeding behaviour was totally disrupted by the lesions of the vomeronasal nerve, whereas lesion of the olfactory nerve had only minor effects on attacks on prey and subsequent ingestion. These results indicate the importance of the vomeronasal system in prey-recognition and subsequent

capture by actively hunting snakes.

Kardong (1975) suggested that prey-capture (in the cottonmouth snake) may be descriptively sub-divided into several temporal phases. These were as follows: search, approach, gliding, striking, biting, release and post-release-activities. In the present study, *N.a. humphreysi* was also observed to exhibit a series of behaviours which may be categorised as several temporal phases; these were search, approach, striking, biting, hooking and arching, and release. Kardong's study did not include observations on searching behaviour; however, Fitch and Shirer (1971) followed a copperhead snake (*Agkistrodon contortrix*) by radiotelemetric methods and found that although members of the genus *Agkistrodon* generally employ ambush techniques during prey-capture, movements within their habitat also occur and a specimen of *A. contortrix* was observed to travel fifteen m in a single activity-period. As described above and, specifically, in Section 2.2, *N.a. humphreysi* is a much more active predator than *A. contortrix* and the searching-phase is of relatively greater importance in relation to prey-capture in tiger snakes than it is in the latter genus.

The approach-phase described by Kardong (*op cit.*) is similar to that observed in the present study. In both cases, snakes orient the head toward the prospective prey and approach it by a series of gradual movements, simultaneously increasing the frequency of tongue-flicking. The approach phase terminates in a noticeably increased degree of "tightness" of the anterior body-coils in both species. The significance of the gradual, intermittent approaching movements is that during stationary periods the head of the snake is maintained in a constant position, whereas the remainder of the body is drawn into loose curves. The increased compaction of the anterior body-coils facilitates the forward-thrusting actions of the head during the strike.

The striking-phase described in the present study of *N.a. humphreysi* is essentially similar to that described in other species by Kardong (1975) and Greenwald (1978). It may also occur in a comparable form in the pythons, which form a "loose S-shaped coil with the forepart of the body" before the strike is delivered (Frazzetta, 1966). Greenwald (1978) stated that "to produce rapid

forward movements of the head in the horizontal plane, no alternative mechanism seems feasible". It would appear then, that this type of striking-technique is widespread throughout many families of snakes, specifically the Colubridae, Elapidae, Viperidae and Boidae and is a common form of behavioural adaptation to prey-capture in terrestrial snakes.

Kardong (*op cit.*) found that as much as 75% of the total body-length of *A. piscivorus* may be directly involved in producing the strike, "depending on the acuteness of the S-shaped body curves". Frazzetta (1966) estimated that in pythons the maximum distance for the delivery of a strike corresponded to 20% of the total body-length of the snake and Greenwald (1978) found that the maximum distance of effective striking in gopher snakes (*Pituophis melanoleucus affinis*) was 22% of the total body-length (however, the mean distance of striking was only 8% of the total body-length). Considering that the *N.a. humphreysi* observed in the present study, performed strikes which involved 8% to 20% of the body-length, it appears that, with the possible exception of the viperids, or at least *A. piscivorus*, less than 25% of the body is regularly employed in the striking actions of terrestrial snakes. In the investigations discussed above, mice were used as prey-items.

In all documented investigations, a series of 'S'-shaped curves of the anterior part of the body of the snake were employed in striking; these curves therefore constitute the part of the body regularly used during the strike. Since Kardong (1975) did not provide estimates of actual distances of the strikes he observed, the relatively high proportion of the body involved in performing strikes by *A. piscivorus*, may have been a consequence of the distance between the prey and the snake exceeding that observed by other investigators, e.g. 8.10 cm (Greenwald, 1978) and 1.5 - 5 cm (the present study).

The velocity of the striking action in *N.a. humphreysi* was slow compared to North American venomous snakes inhabiting warm climates. Van Ripper (1953) demonstrated that the rattlesnake *Crotalus viridis* had an average strike-velocity of 246 cm/sec when attacking over a distance of six cm. The maximum speed that the same author recorded was 277 cm/sec. The gopher snakes (*P.a. affinis*) investi-

gated by Greenwald (1974) produced strikes with an average velocity of 90 cm/sec and a maximum velocity of 175 cm/sec over a distance of five cm. By comparison, *N.a. humphreysi* performed strikes with a much lower velocity, i.e. \bar{x} velocity = 63.6 cm/sec and \bar{x} distance = 2.24 cm.

Although there have been no documented attempts at explaining differences in the velocity of striking in different species of snakes, it is possible that several factors may be involved in determining the actual speed of the process. Firstly, the general morphology of an individual, or species, may be directly related to its ability to produce a rapid strike. A sleek, slender snake would presumably offer less wind-resistance than a large, bulky individual and may, consequently, be able to produce a more rapid strike. However, in the studies discussed here, some anomalies appear to exist. For example, although gopher snakes have a much more slender body-form than tiger snakes and, as expected, produce more rapid strikes, rattlesnakes, which are equally robustly constructed as the tiger snakes, nevertheless produce strikes of much higher velocity than either of the other two species mentioned. Therefore, it is possible that the heavier musculature possessed by the rattlesnake (compared to that of the gopher snake) may be responsible for the more rapid striking-action of the former species. Other factors, discussed below, may be responsible for the differences between the warm-climate and cold-climate species.

Secondly, the adaptations of species of snakes to the prey-species they utilize and the habitats they use may also play a major role in the observed differences in the velocity of striking. It has been established that rattlesnakes feed on small rodents (Van Ripper, 1953) as do gopher snakes (Greenwald, 1974) and both types of snakes have been recognised as active hunters as well as ambush-predators. Consequently, these snakes may require the use of more rapid striking-techniques than *N.a. humphreysi* which feeds mainly on frogs and, as experimental series three (of the present study) illustrated, may feed predominantly in the burrows of the prey-species. In view of this, snakes feeding on active mammals, under open conditions would probably have to employ more rapid strikes than a species such as *N.a. humphreysi* which is more likely to feed in enclosed conditions where escape of the prey is greatly restricted.

A third factor that may be important in effecting the difference in velocities of striking by snakes is temperature. The effect of temperature on the speed of striking has been investigated in one species of gopher snake by Greenwald (1974) who was able to show that as body-temperatures of the snakes increased, the speed and accuracy of the strike were enhanced. Since both gopher snakes and rattlesnakes are essentially warm-climate reptiles regularly experiencing higher environmental temperatures for longer periods than tiger snakes, it appears probable that their capacity for high levels of activity, and performing normal metabolic functions, are higher than those of the tiger snakes. Consequently, the striking velocity may be expected to be higher in the warm-climate species than those occurring in relatively cold climates. The differences in the velocity of striking in different species of snakes may be a consequence of any of the individual factors postulated above or they may result from combinations of any of these and perhaps other, unrecognised factors.

The biting-phase observed in the present study was similar to that observed by Kardong (1975), and consisted of an engulfing movement, using the upper and lower jaws of the snake to encircle the body of the prey. In both studies, the jaws of the snakes were opened shortly before engulfing the prey (but after the strike had been initiated). The hooking and arching actions identified in the present investigation followed successful striking and biting in *N.a. humphreysi*.

The variation in the intensity of post-strike prey-encirclement observed in *N.a. humphreysi*, in the present study, has been documented by other investigators. Greenwald (1978) observed similar prey-encirclement behaviour in gopher snakes but the intensity of the encirclement was much higher; in that "once the prey is encircled, the snakes appear progressively to tighten the coils, not releasing it until it is dead. Often the head of the snake itself is partially obscured from view by the body coils". Willard (1977) described the encirclement of prey by several species of colubrids (including gopher snakes) and boids, in substantial detail. Willard (*op cit.*) defined numerous techniques by which the animals encircled (or constricted) their prey and a comparison of these with the encirclement method employed by *N.a. humphreysi* suggests that the

hooking and arching technique does not function as a constricting or restraining (within the body coils) method of prey-capture. The purpose of these behaviours was investigated in Experiments II and III.

The release-phase observed by Kardang (1975) appears to be more decisive and voluntary than the release-phase observed in *N.a. humphreysi* during the present study. Kardang (*op cit.*) made no mention of struggling or associated escape-behaviours performed by the prey following a successful bite. The release of prey observed in the present study was usually the result of efforts made by the struggling prey itself and occurred 33.3% of all recorded episodes. Kardang provided no data about the relative proportions of releasing actions but stated that "often the prey is not immediately released after a bite but is retained in the jaws until death". The release behaviours observed in Kardang's and the present study, were similar in most essential respects. If the prey was released while it was still alive, the snake usually assumed a pre-striking posture, whereas if the prey was dead before release occurred it was relinquished less rapidly and ingestion generally followed immediately.

Neither colubrids nor boids usually practise release of their prey before death occurs because constriction is their principal technique for restraining and, in many cases, also for killing their victims. The fact that *A. piscivorus* releases its victims (apparently voluntarily) after envenomation may be related to the potency of the venom itself, i.e. death after envenomation, of the mammalian prey, occurs very rapidly in crotalines (Bellairs, 1969). However, since the venom of *N.a. humphreysi* has very little effect, in terms of immobilising poikilotherms, releasing the prey may result in its escape in a natural situation.

With respect to orientation of biting in *N.a. humphreysi* there appeared to be a marked predilection for biting at the anterior parts of the body of the prey; this occurred much more often than biting at the posterior regions. However, the striking distances recorded in relation to specific regions of the body suggest that snakes were usually much closer to the head and pelvic regions at the time of striking than to the mid-body regions. Considering

that the accuracy of striking diminished as distance from the prey increased it seems probable that the closer a snake can approach any given region of the body of the prey, the more likely that a successful strike would be delivered to that region. Therefore, if the snake is able to approach to within a shorter distance of the head and pelvic regions than it can approach to the mid-body regions, then the former regions may be expected to receive the majority of bites.

The striking distance and strike-orientation are probably symptomatic of accurately oriented strikes in many instances. For example, bites delivered to the thoracic region of the prey's body may be inaccurate strikes which were initially oriented toward the head of the prey while the prey was facing toward the snake. This may also be the case with bites oriented toward the pelvic region, some being inaccurate and consequently connecting the lumbar region when the prey was facing away from the snake. The above hypothesis is supported by the data concerning relative proportions of bites delivered to each region.

Any advantage accruing to the snake in terms of latency to the death of the prey resulting from the positioning of bites at different regions of the body of the victim appear to be minimal. From the results obtained in the present study, it appears that the orientation of the bite is a function of "convenience" in that a snake generally strikes at the part of the body which is closest to it at the time of the release of the strike. Similarly, there appears to be no clear advantage to the snake in terms of orientation of the prey during ingestion and the duration of the ingestion process. The position of the prey at the time of ingestion is probably related to the initial position of the bite more than any other factor.

The backward-dragging behaviour observed in *N.a. humphreysi* has not been documented in other elapids. In the present study, the purpose of this behaviour was not fully elucidated; however, it is considered to be an artefact in the method of prey-capture under natural conditions. Therefore, the action is presumably an adaptation to withdrawing the prey from burrows, or from within debris, in order to facilitate unobstructed ingestion, and/or to reduce the susceptibility of the snakes to predation which is increased while its

head is within the burrow.

The actual expression of the ingestion behaviour previously described is considered "typical" of this type of activity in snakes. Its significance, in terms of evolutionary adaptation and kinetics of the jaws, has been discussed in detail by Gans (1961). In the context of the present study it needs only be noted that this is the most efficient and most widely-used method of ingestion, occurring in the majority of species of snakes and it involves a virtual dislocation of the lower mandible in order to facilitate the ingestion of large prey which must be swallowed whole. Although slight variations in technique are known to occur, the general process is similar in all snakes.

The post-ingestive "yawning" behaviour described in the present study is considered to be a means whereby snakes restore the original position of the mandibular bones which were dislocated during ingestion (Bellairs, 1969). This process, therefore, permits the jaws to be returned to their pre-ingestive state and thereby be capable of performing further biting and ingestive behaviour. The ten animals observed to adopt coiled postures following ingestion, may have been practising thermoregulation, attempting to increase their metabolic rates and subsequent digestion-rates. However, no documented information is available regarding post-ingestive thermoregulatory behaviour and any theories relating to the significance of such activities are, at present, merely speculative.

The inability of *N.a. humphreysi* to accomplish successful capture of prey when frogs and lizards were used as the prey-species offered in open conditions, appeared to be a consequence of two relevant factors. Firstly, the natural prey-species were much more adept at escaping, on the approach of the predator, than the laboratory mice. Secondly, the snakes appeared to be conspicuously inept at locating potential prey-species. These observations conveyed the impression that under natural conditions, the movements of prey would have to be substantially restricted, perhaps by the presence of natural obstacles before the predator may be able to effect a strike and successful capture. The fact that each of the snakes used in this particular experiment successfully captured a laboratory mouse following the "natural prey" exercise, indicates

that the feeding drive was adequate but the ability, at least under open conditions, was not.

3.6.2 Experimental Series II

The initial searching behaviours exhibited by the subjects observed in this series of experiments were similar to those exhibited during searching periods in experimental series I and observations on foraging recorded in the field. The increased frequency of tongue-flicking observed when snakes approached the artificial burrow was similar, and probably directly comparable to the increase in frequency of tongue-flicking noted under natural conditions, i.e. when snakes approached and investigated natural obstacles.

The post-striking behaviour observed in this series of experiments indicated a possible adaptive significance of the hooking, arching and backward-dragging observed in previous test-sessions. Both the hooking and arching of the anterior portion of the body resulted in the prey being physically forced to the floor-wall junction of the burrow, thereby apparently restricting the struggling activities of the prey. One result of this type of behaviour was that release of the prey did not occur in any episode of prey-capture. From these observations it appears that the function of the hooking and arching actions is to force the prey into a position where maximum immobilization by the snake can be accomplished. By so doing, the snake compensates for the lack of the instantaneous killing potential of the venom when poikilotherms are utilized as prey.

The observation that the majority of ingestion activity occurred after prey had been withdrawn from the burrow suggests that the backward-dragging behaviour is probably an adaptation directly relevant to killing within a burrow. In a confined space the prey may thereby be held until it is dead, or otherwise ceases to struggle, and can then be removed to more open conditions. After withdrawal from the burrow further manipulation and ingestive "jaw-walking" actions can be accomplished unimpaired by the spatial restrictions existing within the burrow.

Generally, these results indicate that the burrow is perceived as a source of potential prey and re-entries to the burrow indicate that the feeding drives of the snakes were sufficiently strong to promote repeated attempts at capturing prey.

3.6.3 Experimental Series III

The searching behaviour observed in this series of experiments was also similar in most details to the investigatory foraging activities previously observed. Although the rapid-strike techniques observed in this series of experiments were similar to those observed in previous exercises in the present study, the slow engulfing method of prey-capture differed markedly. The latter technique appears to indicate an adaptation to killing within burrows or, at least, to despatching prey within confined spaces. The fact that frogs remained stationary on the floor of the burrow, even during attack suggests that escape was not feasible. When compared to experiments in open conditions the behaviour of both the prey and the predator differed considerably.

The general technique of slowly engulfing prey at close range is probably not adaptive to killing in open situations where considerable speed is required in order to capture prey that may escape at relatively slight provocation (as demonstrated in earlier experiments in the present study).

The hooking, arching and backward-dragging observed in this series of experiments clearly indicate their application as adaptations to the capture of prey within a confined space, such as a burrow. In all observed trials, the frogs were securely restrained by being forced into the corner of the burrow. Consequently struggling by the prey was minimal.

3.7 SUMMARY

The objectives of this series of experiments were to investigate under laboratory conditions the general feeding behaviour of *N.a. humphreysi*. The first series of experimental tests was designed to elucidate the general techniques employed as well as the time relations and kinematics of prey-capture occurring in an open situation (i.e. a substrate devoid of obstacles). The results of these experiments indirectly suggested the design of the apparatus employed in Experimental Series II. This was because several forms of behaviour that were exhibited by the subjects used in previous experiments indicated that the snakes may regularly feed in confined spaces in natural situations.

The results of Experimental Series II also indirectly induced the construction of a more naturalistic type of experimental apparatus in order to facilitate the investigation of the possible function of prey-capture activities observed in Experiments I and II. During the experiments performed under naturalistic conditions, the predators exhibited several distinctive forms of stereotyped behaviour which strongly suggested that they feed mainly in burrows, or other confined spaces in natural conditions.

GENERAL CONCLUSIONS

The results obtained in the course of investigations of the thermal ecology of *N.a. humphreysi* clearly indicated that this species can be considered a thigmothermous poikilotherm conforming to the definition of such a form proposed by Heatwole (1976). Although the subjects were found to be active under conditions of cloudy skies, as well as under clear, cloudless skies, the body-temperatures recorded in the field suggested that the species relies, at least partly, on direct radiation during its thermoregulatory periods. The direct radiation is probably utilised directly, i.e. by exposure of the dorsal surface of the snake as well as entry by conduction through the warming substrate. It appears probable that this species achieves heat-exchange with its surrounding environment through direct radiation, conduction and convection, as do most terrestrial snakes.

The observation that the body-temperature of *N.a. humphreysi* was more closely related to the temperature of the substrate clearly indicates that the animal thermoregulates to a level where its body-temperature is closest to the more stable of the several environmental temperatures. By doing this, it is able to perform its normative activities with less overt thermoregulatory behaviour (after the body-temperature reaches or approximates the optimal level) than an actively thermoregulating homeotherm. Consequently, fluctuations in the amount of shade due to variable amounts of cloud-cover, may have little effect on the body-temperature of the animals as long as the temperature of the substrate remains sufficiently high to permit suitable body-temperatures to be maintained.

The fact that *N.a. humphreysi* relies, at least to some extent, on direct irradiation as a means of obtaining heat, was demonstrated during the various forms of basking behaviour exhibited by subjects observed in the field. Although the coiling posture adopted by the snakes may be related to the prevention of loss of heat obtained through conduction, the frequently observed behaviour of flattening

the body must be interpreted as being related to direct utilization of radiation. Further to this, the observation that at least one subject interrupted its foraging activities and performed the flattening action in an isolated, sunny area of its habitat, indicates an apparent close association between this type of behaviour and direct radiation.

It may be concluded from the above observations, that *N.a. humphreysi* is a typical thigmothermous reptile maintaining its preferred, or optimal foraging body-temperature in a close relationship with the temperature of the substrate. However, this species does not appear to rely fully on substrate-temperatures for thermoregulation but is capable of, and indeed has been observed to utilise direct radiation presumably for raising or maintaining suitable body-temperatures.

From the results obtained in the present study it appears that if any relationship exists between body-temperature and individual size, it is in the form of a tendency for smaller animals to maintain higher body-temperatures. Although this trend is not clearly defined and possibly unacceptable in a strict statistical sense, it clearly suggests that larger animals do not have higher body-temperatures. Since other investigators have concluded that no significant correlation exists between the individual size of snakes and their body-temperatures, and because the trend discovered in the present study is rather vague, it may be concluded that only slight or no such relationship exists. However, if a relationship is recognised to occur, it consists of smaller animals having higher body-temperatures.

It is difficult to determine, at least from the results of the present study, the significance of a mean difference in body-temperature of 0.05°C between male and female subjects. Probably of greater importance is the difference in the general trend of body-temperatures occurring in both sexes. The fact that environmental (and specifically substrate) temperatures are better indicators of simultaneously maintained body-temperatures in males than in females suggests that the sexes differ with respect to thermoregulatory processes or capabilities. As previously mentioned, many theories have been advanced in attempts to explain this phenomenon; however,

until more intensive investigations are undertaken, the precise reasons for such differences will remain merely postulative. It is sufficient to state that the present study has demonstrated that female specimens of *N.a. humphreysi* possesses similar thermoregulatory characteristics to the females of other species of snakes and that the trend appears to be universal within the order.

Field-records based on individual measurements clearly showed that *N.a. humphreysi* maintains a wider range of body-temperature, during bouts of activity than related species occurring in continental Australia. Although the mean maximum body-temperature of *N.a. humphreysi* was somewhat lower than that of related species, the range within which active forms of behaviour were found to take place was 50% greater. This indicates that *N.a. humphreysi* is well adapted to existence in a cold climate, being able to perform foraging activities at body-temperatures below those representing the thermal minima of related species.

The general observations recorded in the field suggest that *N.a. humphreysi* is an actively foraging predator and is unlikely to use ambush- or pursuit-techniques when capturing its prey. Individuals may forage over a distance as little as four m and as great as 50 m (and possibly further) in the course of a single bout of foraging-activity. From the results of the field-investigations, it may be concluded that the major prey-species selectively utilized by *N.a. humphreysi* in the Lake Sorell-Lake Crescent study-area is *L. ewingi* and other species of frogs and perhaps lizards may supplement the diet of the snakes. Lizards are probably utilized as prey-species mainly in the early summer when the majority of frogs are engaged in breeding activities in deep water and, consequently, not readily accessible to the predators.

The types of terrain, or habitat, over which the snakes were observed to forage, in the Lake Sorell-Lake Crescent area varied considerably. However, the principal type of habitat utilized by individuals as home-sites consisted of rock-outcrops. From the information obtained through field-investigations it may be suggested that *N.a. humphreysi* prefers to establish permanent home-sites on or under outcrops of rock. The adaptive advantage of this is probably related to the fact that the rate of cooling of the rocks

is lower than that of any other type of substrate used as potential home-sites (e.g. fallen timber) occurring within a representative area.

The characteristics of permanent home-sites such as those described in the present study are presumably directly related to the daily general activity-patterns of the animals. The basking-pads and short trails are probably associated with the thermoregulatory activities exhibited by the snakes under natural conditions. These types of behaviours may occur at any given time of day (between sunrise and sunset) since the animals were noted to be active between 0900h and 1700h, with a slight peak in activity around mid-day.

The results of the observations made in the field have indicated that populations of *N.a. humphreysi* which exist in close proximity to human activities may experience culling-pressures and these may alter their population-structures more than those of populations that are further removed from such activities. It was not an aim of the present study to formulate conservation-strategies relevant to the tiger snake. However, the fact that the snake population at Silverplains Creek where culling occurs, exhibited a lower ratio of females to males, as well as a smaller biomass than the population studied at Brownwater Lagoon, suggests that the future of the snakes at Brownwater Lagoon may be less precarious than that of the Silverplains Creek population. If the currently prevailing culling-pressures were to continue over a long period of time and if human activities were to continue increasing over that period, the ultimate consequence may be the eradication of tiger snakes within the former area.

The initial experiments performed under laboratory conditions conclusively showed that *N.a. humphreysi* exhibits several distinctive stereotyped behavioural events during feeding activities. Some of these (notably foraging behaviour and tongue-flicking actions) were observed in the field whereas other elements of behaviour (hooking, arching and backward dragging) were directly associated with successful capture of prey. Information accumulated in the course of the field-observations and laboratory experiments suggested that the snakes do not kill their prey in open

situations but in fact, despatch them within the burrows of the prey-species or in other confined spaces. The factors substantiating this conclusion are as follows:

1) Foraging-techniques observed in the field consisted of probing around the perimeter of obstacles and entering small openings.

2) Several instances of "yawning" were observed following withdrawal from beneath obstacles.

3) The main prey-species (represented in gut-samples) is not normally active at the same time of the day as the predator is.

4) The inaccuracy of strikes performed at distances exceeding five cm suggested that capture of natural prey in open conditions was unlikely.

5) Subjects were unable to effect the capture of natural prey under open-arena conditions although the level of the feeding drive was probably adequate.

6) The hooking, arching and backward-dragging actions observed in open conditions appeared to serve little purpose in such conditions; indeed, they were probably inappropriate.

7) All animals tested in artificial conditions were able to perform successful kills in complete darkness.

8) All of the burrows of potential prey-species that were examined in the field possessed only a single entrance; consequently escape of the prey was unlikely after the predator had obstructed the entrance with its body.

9) The slow engulfing technique, performed during experiments within burrows, appears to be maladaptive with respect to prey-capture in open conditions.

10) The hooking, arching and backward-dragging techniques were interpreted as being adaptations to killing prey in confined spaces.

As a general overview, it can be concluded from the results of the present study that *N.a. humphreysi* is well-adapted to relatively cold climates, having a greater range of optimal, or preferred, body-temperatures over which daily activity can take place, than related species inhabiting continental Australia. It selectively utilises rocky outcrops as home-sites in preference to logs and burrows in the soil, and the permanent home-sites are characterised by several distinctive features which are related to the thermoregulatory behaviour of the species. Females exert a relatively greater degree of control over thermoregulation than males, as exhibited by females of other Australian and American species of elapid snakes.

From the results obtained from investigations in the field it appears that the general daily activity of these snakes involves emergence from the home-site when temperatures are suitable and possibly when the feeding drive is also adequate. When optimal body-temperatures are attained, the animal moves off to forage for frogs, which constitute the major proportion of the diet of the snakes. Such foraging-activities probably continue until satiation is achieved or low temperatures exert a restraining effect on movements and the snakes then return to their home-sites. Presumably, the principal variations of this range of behavioural events pertain to the activities occurring during mating and in situations of predator-avoidance.

APPENDIX 'A'ANIMALS PARASITISING *N.A. HUMPHREYSI*ORDER ACARINA

During the course of the field investigations incorporating extensive examination of specimens of *N.a. humphreysi* it was noted that some individuals (4 of the 26 examined) carried acarid ectoparasites. These parasites were located on the dorsal surface of the body and were identified as *Aponomma hydrosauria*. Sizes ranged from 3 to 6 cm in width. The animals were lying with their mouth-parts lodged beneath a dorsal scale of the snake in an anterior-facing position.

CLASS TREMATODA

Dissection of five specimens of *N.a. humphreysi*, in the laboratory, revealed that trematode endoparasites occurred within two of these snakes. The trematode *Dolicopera macalpi* (Nicol) was found within the stomach, the oesophagus and, in one individual, within the upper trachea. The three individuals within which numbers of *D. macalpi* were found contained 42, 28 and 11 parasites respectively.

CLASS CESTODA

In addition to the trematodes found in the five snakes dissected, one animal yielded a number of tapeworms identified as *Spirometia erinacei*. These parasites were discovered in a sub-cutaneous location along the sides of the snake's body. They occurred in boluses approximately three cm in diameter at various intervals along the body. A total of eight boluses of *S. erinacei* were discovered; each was characterized by slight haemorrhaging of the effected tissue.

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