CHAPTER 1

INTRODUCTION

PART 1

CHAPTER 1

ECOLOGY AND DEMOGRAPHY AMONG LIZARDS

OF THE FAMILY SCINCIDAE: AN OVERVIEW

INTRODUCTION

The family Scincidae belongs to the Infraorder Scincomorpha
and forms a nearly cosmopolitan group, absent only from Antarctica
and most high altitude areas (Porter, 1972). Greer's (1970) sub-
familial classification of the family Scincidae recognized 73
living genera and 701 species. Fourteen years later 85 living
genera are recognized with about 1,275 species world wide. Since
Greer's (1970) study no less than 12 living genera and 574 new
species have been described (see Cogger, Cameron and Cogger, 1983).
Scincids clearly make up the majority of lizards in tropical regions
and form 50% of the lizard fauna of mainland Australia. Based on
data from Cogger, Cameron and Cogger (1983), about 250 species in
22 genera are Australian, representing 25.8% of the world genera and
19.6% of the world species.

The five largest groups of Australian skinks are *Ctenotus*
(26.4% of the Australian scincid species), followed by *Lerista* (14.8%),
Egernia (10.8%), *Carlia* and *Sphenomorphus* (8.0% each). The genera
Lampropholis and *Hemiergis* which are the basis of the present study
make up only 4.0% and 2.4% respectively of the total species of
Australian skinks. All other genera collectively account for 25.6%
of the reviewed species.

Contemporary ecology emphasizes the following areas:
(1) population ecology, (2) population genetics, (3) demography,
(4) distribution of organisms in space, and maintenance of population

density (Remmert, 1980).

Population ecology deals mainly with a group of individuals of a single species able to exchange genetic material. This basic unit of ecology is called a population. Basic to the theory is the fact that all organisms normally reproduce more offspring than would be necessary to keep the population constant. Hence, this branch of ecology deals with aspects of population regulation. Without regulation, the traditional growth curves describing growth in natural populations would be all but exponential. However, most natural populations show a characteristic sigmoid growth curve and are regulated by density-dependent and non density-dependent effects on natality and mortality. Population density is also maintained by predator-prey systems and by food supply as it relates to population density. These factors, as well as abiotic ones have a bearing on the distribution of organisms in space.

Population genetics is concerned with organisms in a diploid population sharing a common gene pool. It is based on the assumptions that (1) individuals in a population are not identical, i.e. that they do not individually store the total available genetic information of the population, (2) individuals vary with respect to their relative contribution to the genetic composition of the subsequent generation. For organisms that have many generations per year, during a single season the number of individuals adapted to conditions of that season are shown to steadily increase (see Remmert, 1980 for detailed discussion). Differential survival of different phenotypes during developmental time has been shown in the lizards *Uta stansburiana* and *Eumeces obsoletus* (Fox, 1975, 1978; Simbotwe, 1981). Hence population genetics is concerned with the ecological performance of a variety of genotypes that make up a population in space and time, and how changes in genotypic frequencies over generations result in optimal genetic

adaptation to changing environmental conditions. Even under changing climatic conditions, a population can achieve a high rate of reproductive success (Remmert, 1980).

Except for a study on *Eumeces obsoletus* (Simbotwe, 1981), data on natural selection in skinks are virtually non-existent. Authors who speculate about evolutionary strategies and adaption work from the assumption that life history phenomena have an hereditary basis. Verification of that assumption requires a quantitative genetic approach. Simbotwe (1981) noted a similar problem concerning studies of natural selection on meristic characters of a skink. Selection intensity is known to depend on the heretability of the character. The role of different genotypes in a population recently has been well illustrated by Remmert (1980: 111). Hence, for many aspects of reproduction and survival to be illustrated and validated, the application of quantitative and qualitative genetics to studies of lizard life histories is desirable.

Demography deals with the distribution of size and age classes in animal populations. In growing populations, young animals are present in far greater numbers than are old ones. The predominance of young stages becomes more evident the higher the rate of reproduction of the organism. It is also true for many animal populations, including skinks, that the survival curve showing age-class distribution in relation to mortality reveal that mortality is not uniform throughout the life-cycle. For example, death by predation may be higher among juveniles of a species (see also Remmert, 1980: 116 for details). Reproduction affects demographic structure of the population, through recruitment of various age-classes in a population of different sizes and sexes and carrying different genetic information. These theoretical concepts will form the foundation upon which forthcoming chapters will be based.

Studies on population ecology, demography and reproduction have been carried out on temperate species for many years and research in these fields has increased greatly since the mid 1960's especially in America. But these studies have mainly been carried out on lizards in the families Iguanidae and Teiidae. The family Iguanidae includes 50 living genera and about 560 species making it the dominant family of lizards in the temperate regions of the Americas. The family Teiidae with 38 living genera and about 210 species is second to the Iguanidae (see Porter, 1972: 204-209). As new genera and species are described, this pattern is likely to remain the same. As a consequence, the most important studies on population ecology and demography in lizards have been based solely on these two families. The most important empirical studies include: Tinkle (1967); Turner, Medica, Lannum and Hoddenbach (1969); Turner, Hoddenbach, Medica and Lannum (1970); Tinkle (1972); Tinkle and Ballinger (1972); Ballinger 1973); Parker and Pianka (1975); Van Davendar (1983); Vinegar (1975); Whittaker and Goodman (1979) and Dunham (1981, 1982).
Very few comparative studies have been carried out on species in the family Scincidae. The only studies on population dynamics and demography are those by Alcala and Brown (1967) and Barbault (1967) on annual cycles in biomass at Lamto, Ivory Coast, Africa. Barbault (1974a,1974b, 1974c, 1974d, 1976) has published significant work on reptiles of Africa most of which describe population dynamics and structure of skink populations in savannas (see also Barbault, 1974e, 1975a,1977, 1983 on similar topics). Barbault and Lecordier's (1977) work, including those cited earlier, provided a solid theoretical background upon which concepts of population ecology of the skinks and other reptiles of savanna ecosystems can be evaluated, and various hypotheses drawn from theoretical data were tested.

Major ecological studies on skinks from various parts of the world include those of Huey and Pianka (1977a, 1977b) and Huey, Pianka, Egan and Coons (1974) on mabuyas of the Kalahari desert, southern Africa, that of Evans and Evans (1980) on mabuyas of Praslin Island, Seychelles, and Brooke and Houston (1983) on mabuyas of Cousin Island, Seychelles. The only comparative studies on skinks of Australia have been those by Barwick (1965) on *Egernia cunninghami* and Pengilley (1972) on lygosomine skinks.

Detailed studies of population ecology and demography in the Australian skinks are still greatly needed. In tropical areas (where skinks tend to be best represented) most studies on lizards generally are concerned primarily with reproductive patterns (see Marshall and Hooks, 1960; Chapman and Chapman, 1964; Inger and Greenberg, 1966a; Licht and Gorman, 1970; Marion and Sexton, 1971; Sexton, Ortlep, Hathaway, Ballinger and Licht, 1971; Towns, 1975; Simbotwe, 1980; Schwaner, 1980; Fitch, 1970, 1982). In this thesis, literature data are analyzed in order to compare life history characteristics of lizards that are of tropical distribution with those of primarily temperate species.

MATERIAL AND METHODS

A literature search was carried out in order to gather demographic and reproductive data on skinks from both temperate and tropical regions. Skinks were further classified as, (1) single-brooded or multiple-brooded, (2) oviparous, ovoviviparous or viviparous, and (3) tropical or temperate, in order to update demographic and reproductive information provided by Tinkle *et al.* (1970) and Fitch (1982). Because present analysis is dependent on the reproductive categories provided by various authors (see Table 1),

the classification of modes of reproduction does not follow that of
Shine (1983a) which considers reproductive modes to constitute a
continuum. Even though arbitrary, the present classification helps in
discerning reproductive habits of various species of lizards (see
Tinkle *et al.* 1970).

RESULTS

Table 1 provides demographic and reproductive data of 56 species
of skinks. Data from 56 species of temperate and tropical skinks,
accumulated over a period of 46 years were analyzed. Of these, 23
(41.1%) were of temperate distribution and 33 (58.9%) were tropical.
Minimum size at maturity in females ranged from about 26 mm SVL in
the small Australian lygosomine skink *Lampropholis guichenoti* (see
also Chapter 4) to 107 mm SVL in *Eumeces obsoletus*. Mean size at
maturity ranged from 36 to 136 mm SVL (Table 1). Age at first repro-
duction was as early as 6 months in *Panaspis nimbaensis*, and as late as
36 months in *Eumeces obsoletus* (Table 1).

Data on clutches per season for both temperate and tropical
species were available only from 25 (44.7%) species leaving 31 (55.3%)
unknown. Of the 25 species, 12 were single-brooded whereas 13 were
multiple-brooded.

Out of 25 species of skinks that had complete data on clutches
per season, 10 (44.0%) were temperate skinks and 15 (56.0%) tropical.
A within climate analysis showed that among temperate species 9 (90.0%)
produced single clutches per season whereas 1 (10.0%) produced multiple
clutches. Of the 15 tropical species 3 (20.0%) were single-brooded
and 12 (80.0%) were multiple-brooded.

Data on mode of reproduction were recorded for all 56 species
analyzed. Thirty-eight (67.8%) of the species practiced oviparity,

17 (30.4%) were viviparous and 1 (1.8%) was ovoviviparous. Within

the 23 temperate species, 8 (34.8%) were viviparous whereas 15

(65.2%) were oviparous. Similarly, of the 33 tropical species 8

(24.3%) practiced viviparity and 24 (72.7%) oviparity; only one

(3.0%) was ovoviviparous (see Table 1). There was clearly an increase

in the incidence of oviparity and production of multiple clutches

among tropical skinks whereas viviparity and incidence of production

of single clutches was more prevalent in temperate skinks. A quick

glance at Table 1 shows that mean clutch size ranged from 1 to 13 eggs.

Out of 49 clutches analyzed, mean clutches of 2 eggs were by far the

most prevalent (see Table 1).

Only 7 (12.5%) species had complete demographic and reproductive

data cited whereas 49 (87.5%) did not. Mean adult size, minimum size

at maturity and age at first reproduction were the most infrequently

reported, in ascending order (see Table 1).

DISCUSSION

Climatically, the world can be divided into two main categories,

temperate and tropical. The latter can be either wet or dry (see

Lutgens and Tarbuck, 1979 for details). The family Scincidae is a

large family of lizards of world-wide distribution in temperate and

tropical regions. However, most species and genera are tropical

(Fitch, 1982). According to Greer (1968: 71) 95 viviparous species

and 152 oviparous species are known. These numbers may have changed,

but the trend remains the same. While most genera tend to be

exclusively viviparous or exclusively oviparous, *Eumeces, Leptosiaphos,*

Mabuya and *Sphenomorphus* include species of both types. The data in

Table 1 agree well with those of Tinkle *et al.* (1970) who found that

large lizards maturing late in life tend to have larger clutches

than early-maturing, small lizards. The present data with those of
Tinkle *et al.* (1970) collectively show that skinks seem to have by
far the largest relative number of species that mature at an age
younger than 12 months.

Data on modes of reproduction provided interesting results
which concur with results obtained by other authors. Though no
single author has shown conclusively that cold climates have promoted
greater incidence of viviparity (see Shine, 1983b: 404 for a detailed
discussion of the "cold climate hypothesis") in lizards generally,
the present study (see Table 1) has shown conclusively that in the family
Scincidae, viviparity and production of single clutches are a definitive
feature of temperate species whereas oviparity and production of
multiple clutches per season is a characteristic of tropical species.
In temperate species, live bearing may be advantageous (in the sense of
Shine, 1983b) in that uterine retention of eggs accelerates embryo-
genesis and removes the eggs from a nest vulnerable to predation.

Even though oviparity is the predominant mode of reproduction
in both temperate and tropical species, its incidence is greater in
the tropics. This statement agrees well with the present study and
that of Greer (1968).

The many interesting studies in life history patterns including
those of Fitch (1970, 1982), Tinkle (1969), Tinkle, Wilbur and
Tilley (1970) and Tinkle and Gibbons (1977) are merely descriptive
and have their discussions based on speculations concerning what
evolution ought to produce for optimum adaptation other than what
development can produce within constraining factors of ultimate
(genetic), proximate (short-term environmental factors) and mechanical
limitations on development. How all these competing factors, including
simultaneous activities of competitors, predators, parasites, food,

space, and weather shape life history phenomena is hardly clear.

Theoreticians, including Stearns, who study life history, have pointed out how modelling animal life histories can help empirical studies. Theoretical studies of life history have also highlighted problem areas (see Stearns, 1976, 1977).

Even though the number of demographic and reproductive studies in skinks have increased (15 species only cited in Tinkle *et al.*, 1970, compared with 56 in the present study), in the last fifteen years, the majority of authors do not provide the complete demographic and reproductive data necessary for describing life history character-istics. Unfortunately, the trend continues and the situation is no better than it was 15 years ago (see Tinkle *et al.*, 1970, pp 57-61 c.f. Table 1 of the present study).

While analyzing many of the papers cited in Table 1, I have observed that a great deal of work on demography and reproduction has been carried out without reference to any general theory. Tinkle *et al*. (1970) raised questions on reproductive strategies and their diversity and selective values; these have been tested by only one study (see Somma and Brooks, 1976) compared with the numerous studies on skinks cited in Table 1, that have not done so. It is hoped that this review of the family Scincidae will stimulate research on their demography and reproduction, paying attention to the basic data and questions raised by Tinkle *et al*. (1970) fifteen years ago. Data should be subjected to testing of hypotheses within the context of ecology, and development and evolution.

TABLE 1. Demographic and reproductive data on skinks, an updating of tables of lizards by Tinkle *et al.* (1970) and Fitch (1982). S = single-brooded, M = multiple-brooded, O = oviparous, OV = ovoviviparous, V = viviparous, tr = tropical, tm = temperate.

Species	Minimum size at maturity (mm)	Mean size of mature females	Range and clutch size	Age at first re-production (months)	Mode of repro-duction	Clutches per season	Climate	Locality	Sources
Afroablepharus wahlbergi	-	< 65	1-6	-	O	-	tr	E. Africa	Greer, 1974
Anotis maccoyi	-	-	(2-7)	-	O	-	tm	Australia	Robertson, 1976, 1981
Carlia rhomboidalis	-	48	2.0	-	O	M	tr	Australia	Wilholf, 1963
Carlia 30 ± sp	-	< 65	1-6	-	O	-	tr	E. Africa	Greer, 1974
Carlia robustus	-	-	(4-7)	-	O	-	tm	Australia	Way, 1979
Chalcides ocellatus	-	-	(3-8)	-	V	S	tr	Tunisia	Mosauer, 1934
Cophoscincopus durus	-	< 65	2.0	-	O	-	tr	W. Africa	Greer, 1974
Cryptoblepharus boutoni	-	< 65	2.0	-	O	-	tr	Samoa	Schwaner, 1980
Ergernia cunninghami	-	-	(3-8)	-	V	-	tm	Australia	Barwick, 1965
Emoia atricostata	-	80	2.0	9	O	M	tr	Philippines	Alcala & Brown 1967
Emoia cyanura	-	-	2.0	-	O	M	tr	New Hebrides	Baker, 1947
Emoia werneri	-	-	2.0	-	O	M	tr	New Hebrides	Baker, 1947
Emoia nigra	-	-	2.3	-	O	-	tr	Samoa	Schwaner, 1980
Emoia samoensis	-	-	5.3	-	O	-	tr	Samoa	Schwaner, 1980
Eumeces egregius	40	-	4.8	12	O	S	tm	Florida	Mount, 1963

Table 1 (Cont'd)

Species	Minimum size at maturity (mm)	Mean size of mature females	Range and mean clutch size	Age at first reproduction (months)	Mode of reproduction	Clutches per season	Climate	Locality	Sources
Eumeces fasciatus	65	-	9.5	24	O	S	tm	Kansas	Fitch, 1954
Eumeces obsoletus	107	-	11.4	36	O	S	tm	Kansas	Fitch,1955,1967
Eumeces obsoletus	79	103.0	12.2	-	O	S	tm	N. America 42(N) Latitude	Simbotwe,1978
Eumeces obsoletus	83	102.0	11.9	-	O	S	tm	N. America 39(N) Latitude	Simbotwe,1978
Eumeces obsoletus	78	102.8	9.3	-	O	S	tm	N. America 36(N) latitude	Simbotwe,1978
Eumeces obsoletus	74	97.2	10.0	-	O	S	tm	N. America 33(N) latitude	Simbotwe,1978
Eumeces obsoletus	77	103.1	13.1	-	O	S	tm	N. America 30(N) latitude	Simbotwe,1978
Eumeces septen- trionalis	65	-	8.8	36	O	S	tm	Minnesota	Brecknridge, 1943
Eumeces skilto- nianus	58	64	4.4	30	O	S	tm	California	Tanner, 1957
Geomyersia glabra	-	< 65	1.0	-	O	-	tr	Boungainville Island	Greer, 1974
Hemiergis decresiensis	-	-	(2-4)	-	V	-	tm	Victoria Australia	Robertson, 1976,1981
Hemiergis decresiensis	48	56	2.4	11	V	S	tm	Newholme Australia	Present study
Hemiergis peroni	-	-	(1-6)	-	V	-	tm	Australia	Smyth, 1968

Table 1 (Cont'd)

Species	Minimum size at maturity (mm)	Mean size of mature females	Range and mean clutch size	Age at first reproduction (months)	Mode of reproduction	Clutches per season	Climate	Locality	Sources
Lygosoma laterale	35	-	2.5	9	O	M	tm	Florida	Brooks, 1967
Lygosoma laterale	40	-	3.3	12	O	M	tm	Louisiana	Johnson, 1953
Lygosoma laterale	38	47	3.8	12	O	M	tm	Kansas	Fitch & Greene, 1965
Mabuya striata	72	84	4.2	12	V	M	tr	Mosi-oa-Tunya National Park	Simbotwe, 1980
Mabuya striata	73	83	4.4	-	V	-	tr	Kalahari	Huey & Pianka, 1977b
Mabuya quinquetaeniata	87	98	4.8	-	O	M	tr	Mosi-oa-Tunga National Park	Simbotwe, 1980
Mabuya striata	62	70	7.0	12	V	-	tr	Tanganyika (=Tanzania)	Robertson *et al.*, 1965
Mabuya multifasciata	-	-	6.0	-	V	M	tr	Java	Kopstein, 1938
Mabuya mabouya	65	-	3.3	-	V	-	tr	Dominica	Sommer & Brooks, 1976
Mabuya buettneri	-	83	8.4	6	O	M	tr	Lamto Ivory Coast	Barbault, 1976
Mabuya maculilabris	-	65	5.5	6	O	M	tr	Lamto Ivory Coast	Barbault, 1976
Mabuya variegata	39	38	2.1	-	V	-	tr	Kalahari	Huey & Pianka, 1977b

Table 1 (Cont'd)

Species	Minimum size at maturity (mm)	Mean size of mature females	Range and mean clutch size	Age at first reproduction (months)	Mode of reproduction	Clutches per season	Climate	Locality	Sources
Lampropholis guichenoti	26	36	2.6	8.9	O	S	tm	Newholme Australia	Present study
Lampropholis guichenoti	-	> 35	3.0	-	O	-	tm	Corre Flats Australia	Pengilley, 1972
Leiolopisma eutresceauxii	-	-	(1-6)	-	O	-	tm	Australia	Pengilley, 1972
Leiolopisma x. rawlinsoni	-	-	(2-3)	-	O	-	tm	Australia	Pengilley, 1972
Leiolopisma trilineata	-	-	(2-10)	-	O	-	tm	Australia	Pengilley, 1972
Leiolopisma fusca	-	58	2.0	-	O	M	tr	Australia	Wilholf & Reiter, 1965
Leiolopisma aeneum	45	-	2.2	-	V	-	tm	New Zealand	Barwick, 1959
Leiolopisma zelandica	54	-	5.1	24	V	S	tm	New Zealand	Barwick, 1959
Leiolopisma suteri	67	-	3.7	33	O	S	tm	Motutopu Is. New Zealand	Towns, 1975
Lipinia leptosoma	-	< 65	1.0	-	O	-	tr	Palau Islands	Greer, 1974
Lipinia 20 sp	-	< 65	2.0	-	OV	-	tr	Indo-Australian Archipelago Pacific Is.	Greer, 1974
Lipinia vittigera	-	< 65	2-4	-	O	-	tr	S.E. Asia	Greer, 1974

Table 1 (Cont'd)

Species	Minimum size at maturity (mm)	Mean size of mature females	Range and mean clutch size	Age at first reproduction (months)	Mode of reproduction	Clutches per season	Climate	Locality	Sources
Mabuya occidentalis	78	79	6.7	–	0	–	tr	Kalahari	Huey & Pianka 1977b
Mabuya spilogaster	55	70	5.4	–	V	–	tr	Kalahari	Huey & Pianka 1977b
Menetia greyi	–	< 65	2	–	0	–	tr	Australia	Greer, 1974
Menetia greyi	–	–	(1–3)	–	0	–	tm	Australia	Smyth & Smith 1974
Menetia boulengeri	–	–	(2–5)	–	0	–	tm	Australia	Smyth & Smith 1974
Neoseps reynoldsi	45	–	2.0	12	0	–	tm	Florida	Telford, 1959
Panaspis nimbaensis	–	45	2.5	6	0	M	tr	Lamto Ivory Coast	Barbault, 1976
Prasinohaema 4 sp	–	–	9.0	–	V	–	tr	New Guinea	Greer, 1974
Prasinohaema virens	–	–	2	–	0	!	tr	New Guinea and Solomons	Greer, 1974
Pseudomoia spenceri	–	–	(1–2)	–	V	–	tm	Australia	Pengilley, 1972
Sphenomorphus quoyi	–	–	(2–7)	–	V	–	tm	Australia	Veron, 1969
Sphenomorphus tympanum	–	–	(2–5)	–	V	–	tm	Australia	Pengilley, 1972
Sphenomorphus tanneri	41	45	2.0	–	0	M	tr	S.E. Asia	Greer & Parker, 1967
Sphenomorphus charrieri	–	< 65	2.3	–	0	–	tr	Costa Rica	Fitch, 1973a

Table 1 (Cont'd)

Species	Minimum size at maturity (mm)	Mean size of mature females	Range and mean clutch size	Age at first repro- duction (months)	Mode of repro- duction	Clutches per season	Climate	Locality	Sources
Typhlosaurus lineatus	57	136	1.5	20-32	V	S	tr	Kalahari	Huey *et al.* 1974
Typhlosaurus gariepensis	58	122	1.0	20	V	S	tr	Kalahari	Huey *et al.* 1974

PART 2

CHAPTER 1

THE ENVIRONMENT

INTRODUCTION

Australia, with an area of approximately 7.7 million km^2, is
the smallest of the world's continents (Bustard, 1970a). The
continent is characterized by two main physiographic features, (1)
plateaus, and (2) plains. Hence the Australian continent can be
divided further into three major physical regions, (1) great plateau
of the west, (2) the central basin and (3) the eastern highlands.
The concern of the present study is the eastern highlands and table-
lands (Fig. 1) where the study area was located.

STUDY SITE

The general geographic distribution of *Lampropholis guichenoti*
and *Hemiergis decresiensis* is shown in figures 2 and 3. Cogger,
Cameron and Cogger (1983) provided more detailed locality data for
each of these species. However, the present study is based on
populations located at Newholme, Armidale, N.S.W. The study area is
situated at the back of Mount Duval, near Sandy Creek, about 10 km from
the University of New England campus, 13°25'S and 151°39'E. The
predominant vegetation is *Eucalyptus* woodland. The geological features
of Newholme are characterized by numerous granite rock outcrops and
rocky hills which are exposed portions of the New England batholiths
(Challacombe, unpublished notes). The climate is characterized by mild,
rainy springs, hot, rainy summers (> 30°C) and cold winters, (< 0°C)
with snowfalls at higher elevations.

Figure 1. Map of New England, showing the location of

Newholme on the New England tablelands, N.S.W.

Qld.
New England
TableLands
S·A
N·S·W
Vic·
29

0   500   1000
                    km

Lismore

Tenterfield

Grafton

Emmaville
Glen Innes
Inverell
Tinga

30°S

Guyra

Dorrigo

NEWHOLME
Armidale
Ebor
Ballingen
Wollomombi
Uralla

Walcha

31
Tamworth

0   20 40 60 80
                    km

Boundary
of New England
Table Lands

Taree
152°E   151
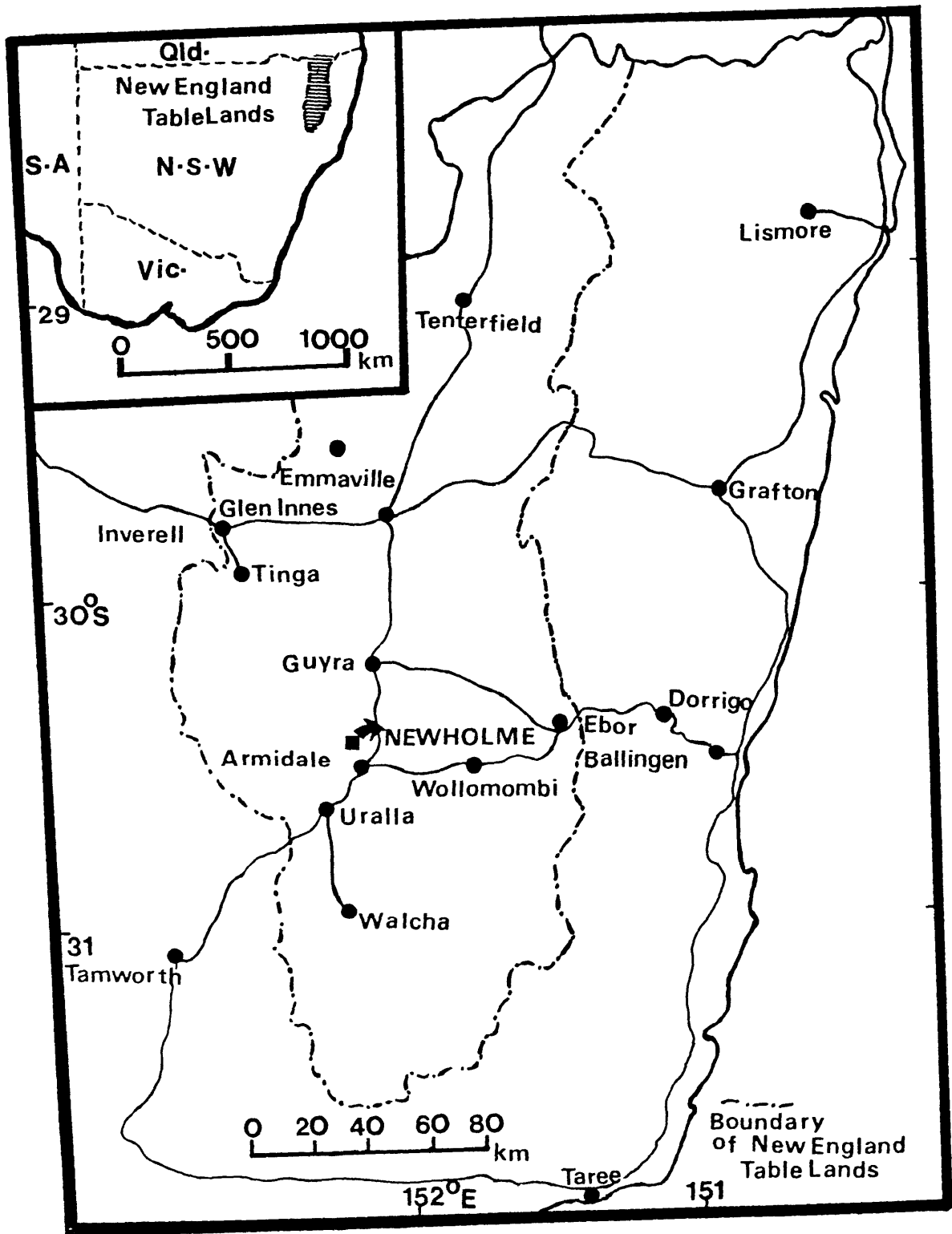
Figure 2. Map showing the geographic distribution of

Lampropholis guichenoti in Australia (after

Cogger, 1975).

WA

SA

NT

VIC

NSW

QLD

TAS
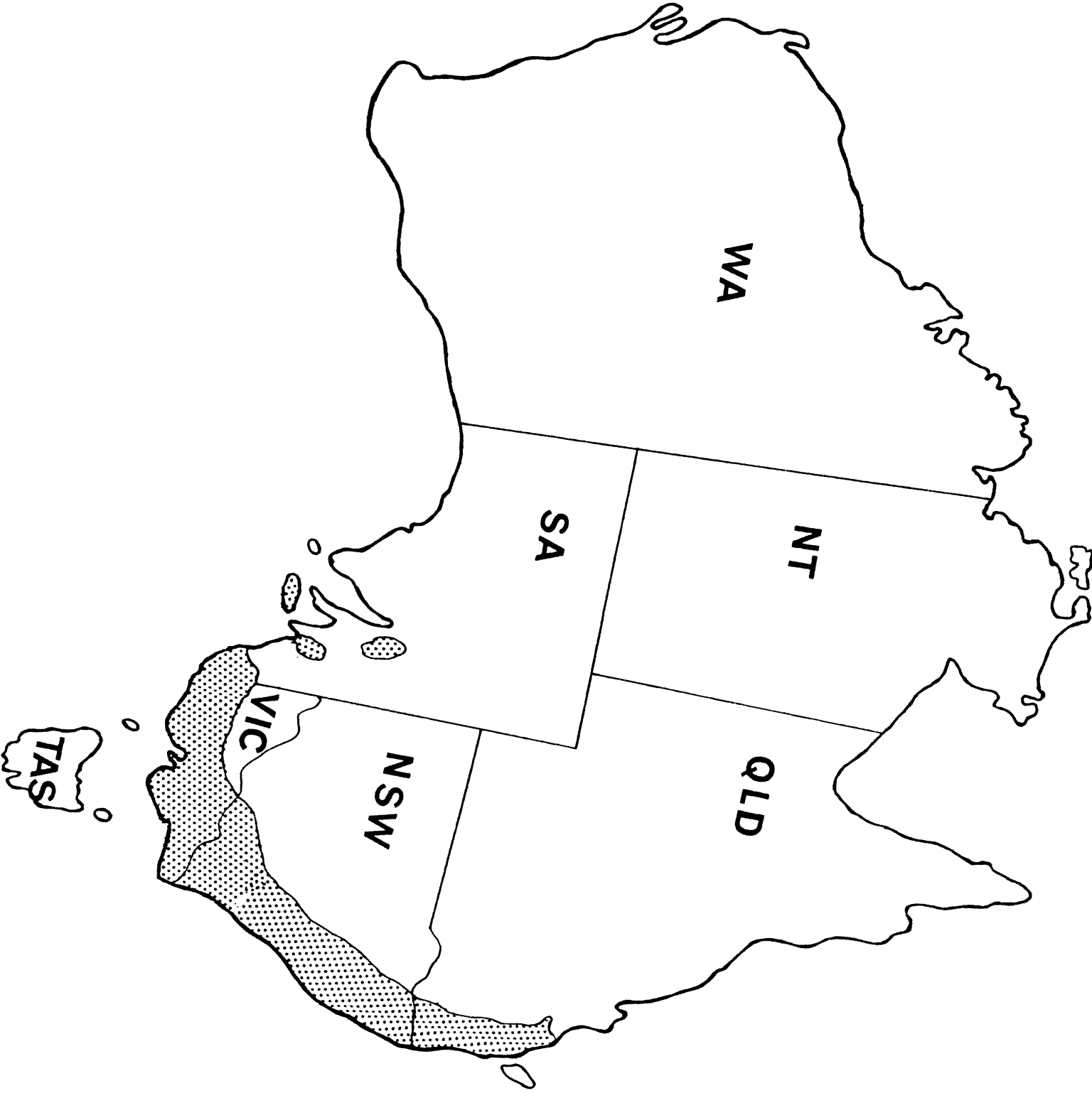
Figure 3. Map showing the geographic distribution of

Hemiergis decresiensis in Australia (after

Cogger, 1975)

WA

NT

SA

QLD

VIC

NSW

TAS
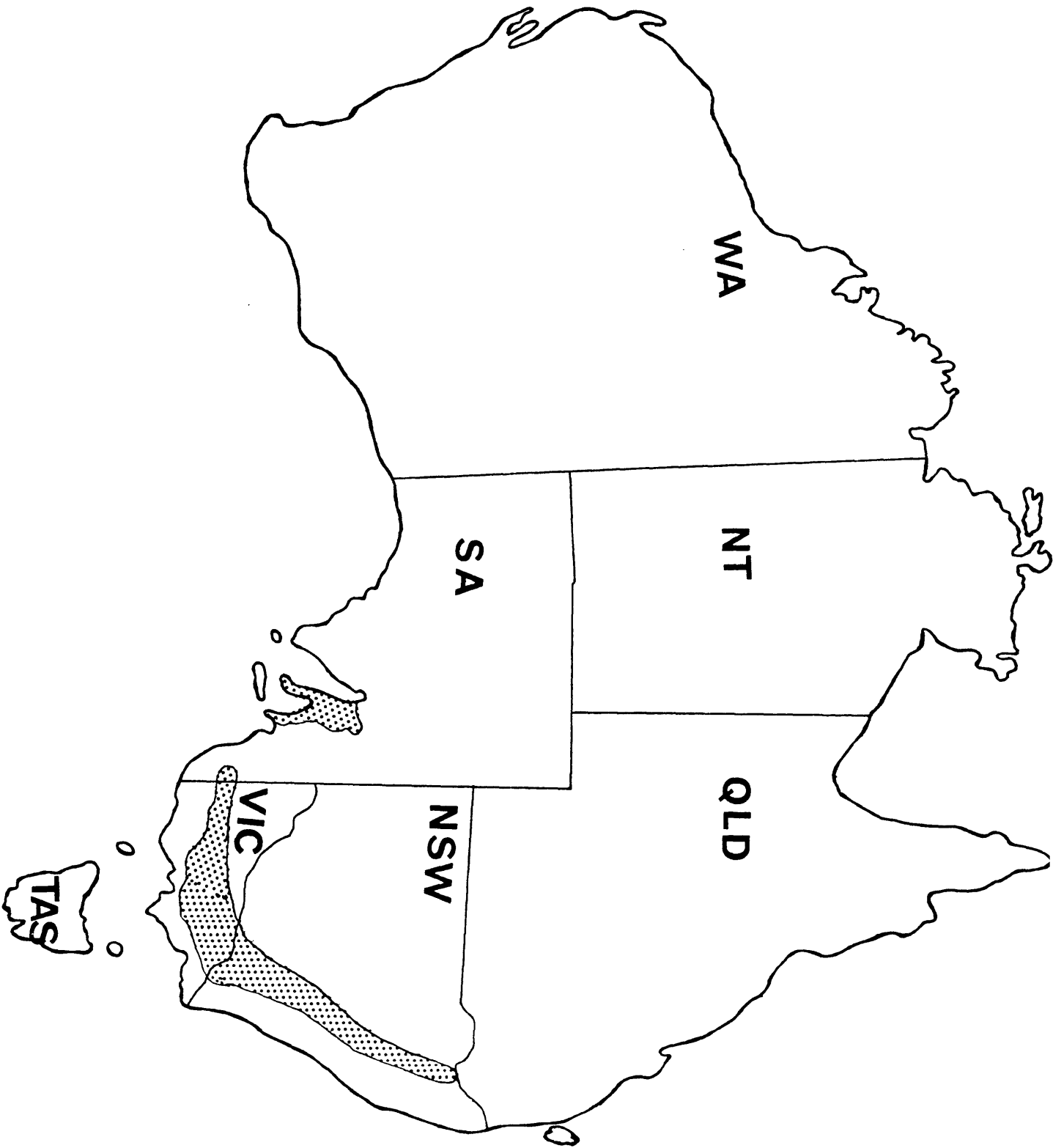
WEATHER

In Australia droughts are a common feature and many elements of the fauna and flora are adapted to survive severe dryness (Bustard, 1970a). The unreliability of rainfall over most of Australia is a greater biological problem than its scarcity (Bustard, 1970a). Weather data used in the present study were collected from unpublished notes at the Newholme Field Station. This study covers the drought stricken years of 1981 and 1982, as well as 1983 and 1984 after the drought had broken. This provided an opportunity for testing in a field situation the effects of drought and the advent of the return of wet conditions, on *Lampropholis guichenoti* and *Hemiergis decresiensis* populations. Figure 4 provides a summary of the total rainfall recorded at Newholme for the years 1981 to 1984. Important fluctuations were observed in the amount of rainfall received in successive years from 1981 to 1984 (see Fig. 4). Figure 5 summarizes temperature data covering 1981 to 1984. Temperatures at Newholme start to rise during spring and reach a maximum in summer months. However, they start to fall in autumn reaching their lowest in winter. These winter temperatures are low enough to cause the animals to become inactive and brumate and in some cases may even result in death.

Based on weather records compiled by Challacombe for Newholme, covering a period of nearly 30 years, a rainfall and temperature graph (Fig. 6) was constructed which shows the patterns at Newholme during the months when animals are active. These graphs reveal that animals are active at the time of the year when both rainfall and temperature are at their peak (see Chapter 2).

Figure 4. Total rainfall at Newholme during the years
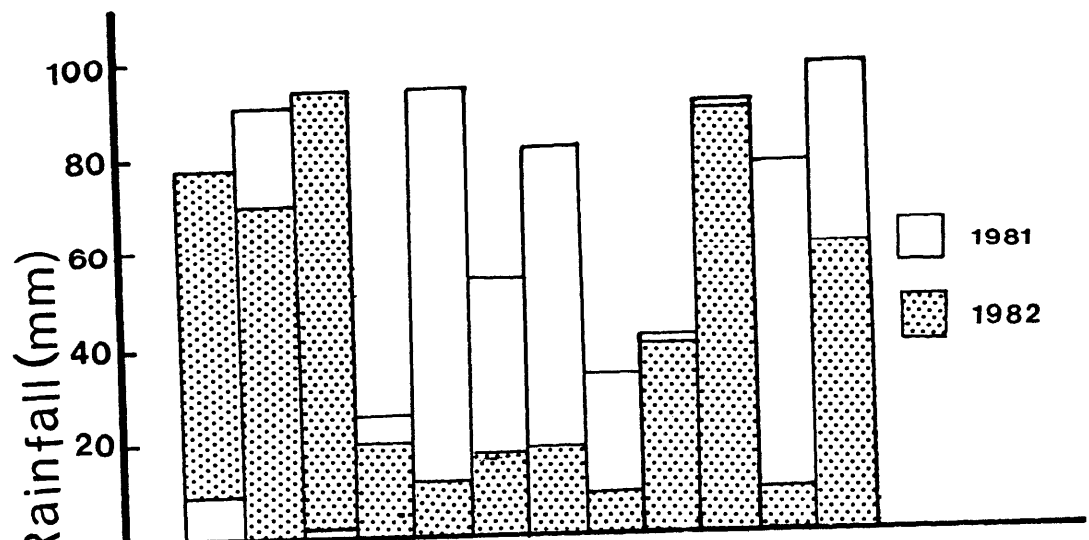1981 to 1984. Data given are only up to the
end of the study.
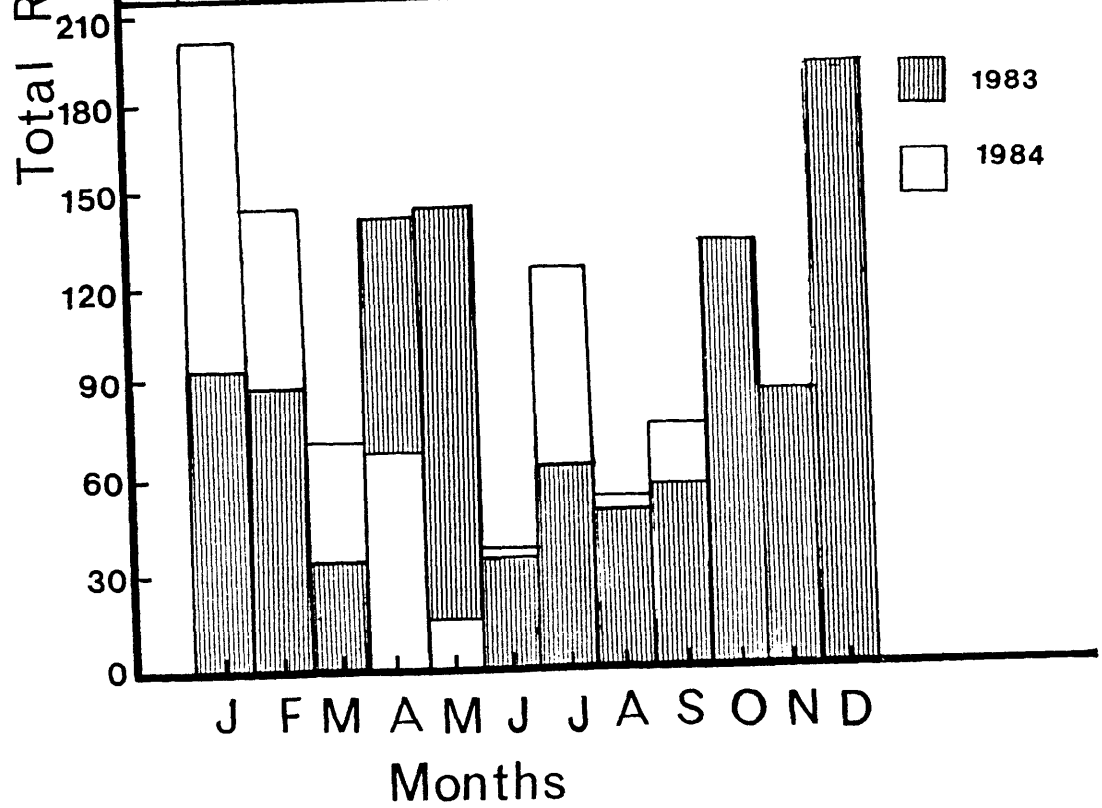
Figure 5.   Minimum and maximum temperatures at Newholme

for the years 1981 to 1984. Data given are

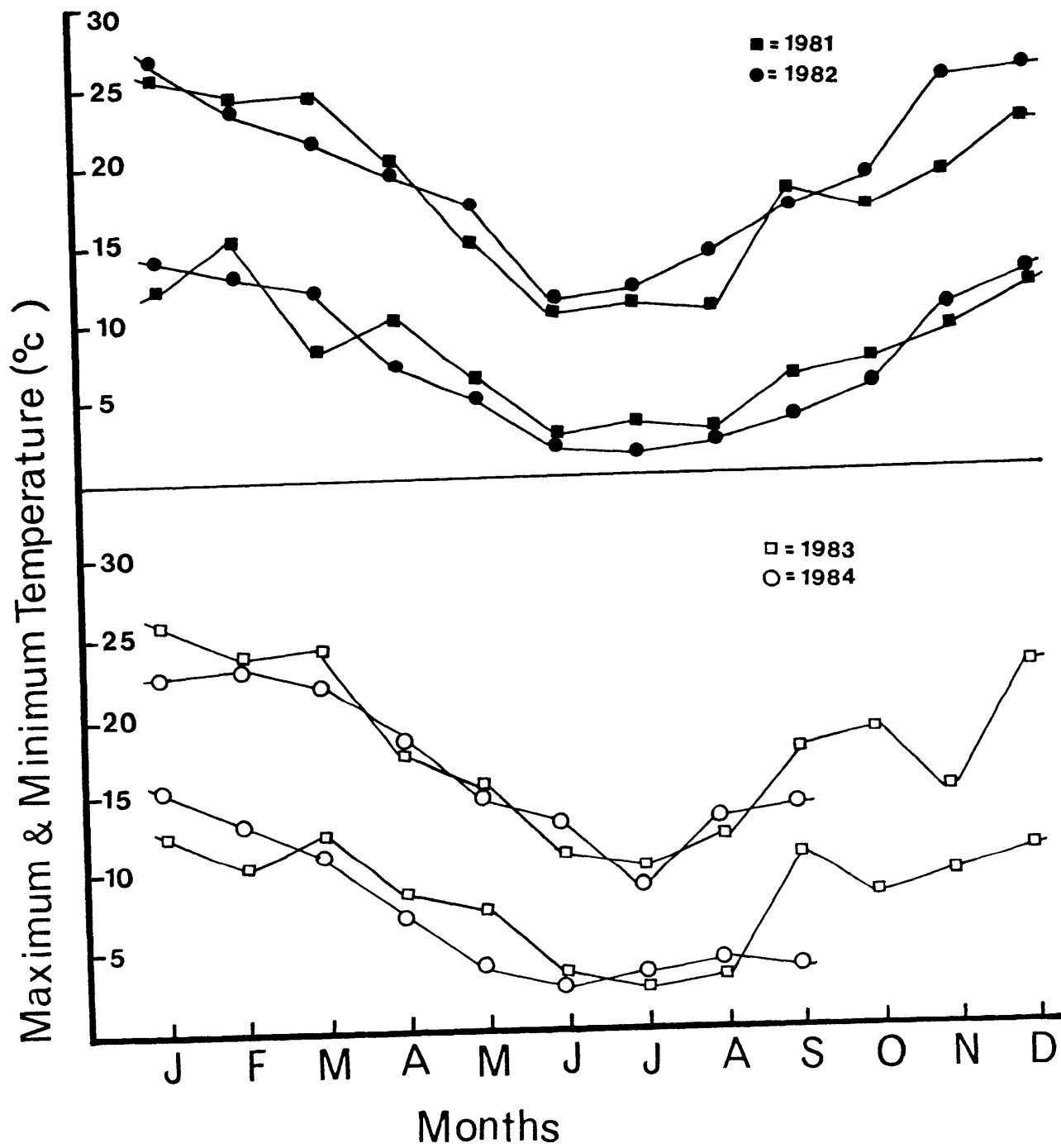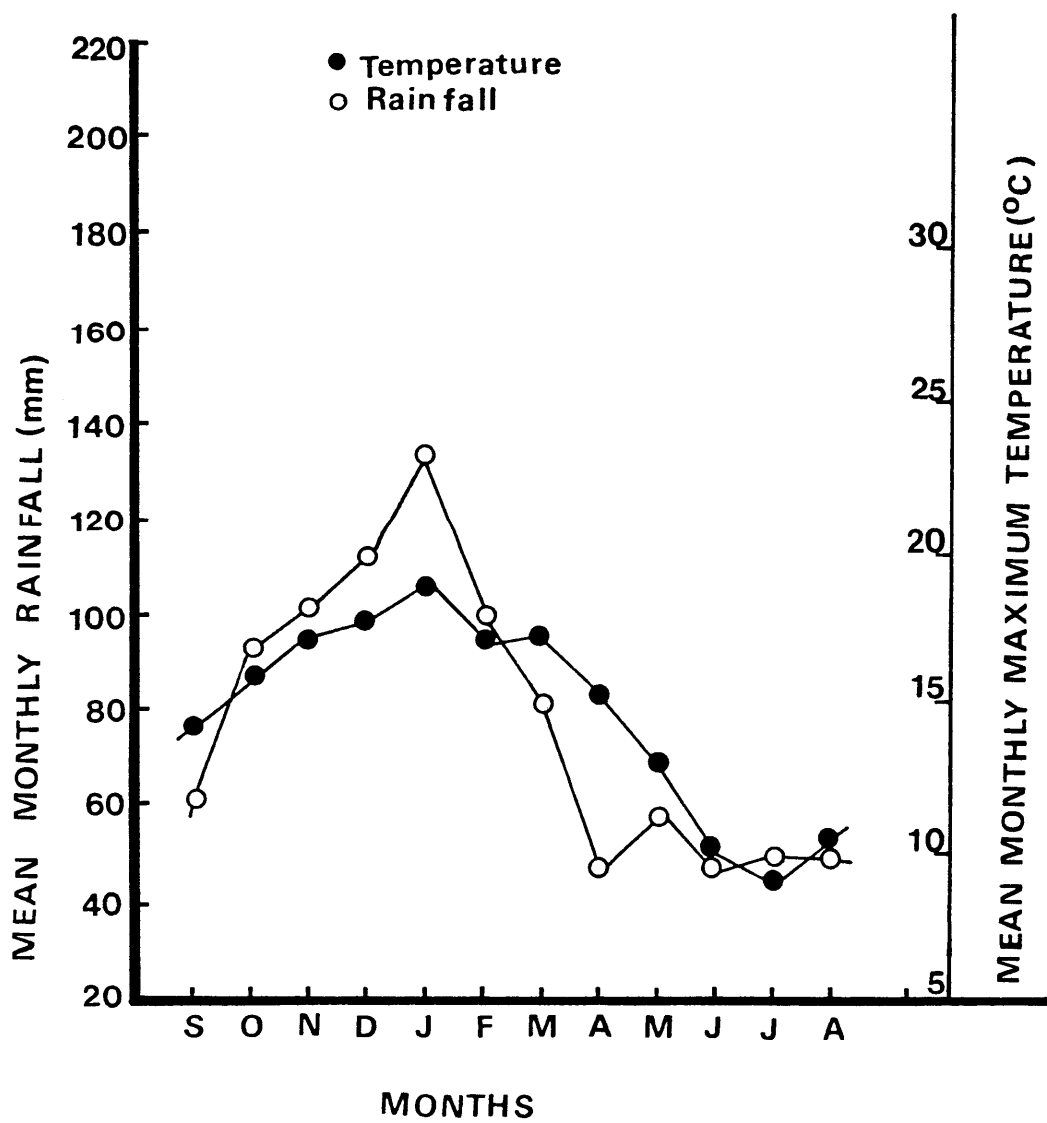only up to the end of the study.

Figure 6. Patterns of rainfall and temperature at Newholme

during times of animal activity.

Data represent means over 30 years.

CHAPTER 2

NICHE RELATIONS

PART 1

CHAPTER 2

TEMPORAL, THERMAL AND FOOD NICHE

INTRODUCTION

Since Hutchinson's (1959) question, "Why are there so many
animals?", research on how similar species divide resources and how
this leads to the natural regulation of species diversity has
increased tremendously (see Schoener, 1974). Studies of resource-
partitioning aim to analyze the limits interspecific competition
places on the number of species that can stably coexist. This kind
of research among coexisting species has attracted considerable
interest and its importance in minimizing actual or potential com-
petition has attracted   many theoretical and empirical studies (see
MacArthur and Pianka, 1966; Levins, 1968; Lack, 1971; MacArthur 1972;
Jenssen, 1973; Pianka, 1973; Cody, 1974; Schoener, 1974; Schoener,
1975; Fuentes, 1976; Lister, 1976 Pianka, 1976a; Simon, 1976; Simon
and Middendorf, 1976; Maury and Barbault, 1981; Ortega *et al.*, 1982).

The limits to the number of species that can coexist were the con-
cern of the mathematical models of Lotka (1925) and Volterra (1926).
Their models were supported by Gause (1934) and many other later
workers who showed, under laboratory conditions, that similar species
tended to cause each other's extinction. This result led to Gause's
principle which states that species can not coexist for long if they
are too similar in their use of the same kind of exhaustible resources.
Hutchinson was the first to conceive of the niche as comprising intervals
of population survival along each resource axis (see Schoener, 1974).
Currently many ecologists consider the niche as the frequency distri-
bution of resource utilization along the various axes.

Early work on measuring niche width used two kinds of measures, (1) indices of the dispersion of a population's resource use over resource categories (Levins, 1968; Colwell and Futuyma, 1971; Pielou 1972), and (2) indices of morphological variation in traits related to food gathering; e.g. head size, mouth gape, bill size (Van Valen, 1965; Jain and Marshall, 1967; Grant, 1967, 1971; Tamsitt, 1967; Wilson, 1969; Soulé and Stewart, 1970; McNab, 1971; Findley, 1973; Derickson, 1976a; Simon 1976, Simbotwe and Garber, 1979). The second measure is possible in most lizards because they lack two major characteristics which are found in mammals, i.e., ability to masticate, and presence of an internal swallowing mechanism (see Smith, 1984 for details). Because of this, among generalist species, large lizards tend to feed on large prey and small lizards on small prey.

Because early ecologists were from temperate areas, most of the theoretical and empirical studies cited above are based on temperate species. Studies based on iguanids and teiids are in the majority (see Chapter 1 for probable reasons). A very interesting and classical study of iguanid lizards by Simon (1976) showed that the lizards she studied seemed to coexist by differing in times of activity, microhabitats or substrate use, thermal behaviour and the type and size of foods eaten. This study and those of later workers provided support for the theory of resource partitioning. Very few studies involving scincids have applied these techniques, exceptions are those of Huey and Pianka (1974) and Huey *et al.* (1974) in the Kalahari desert, Simbotwe and Garber (1979) in southern Zambia, Simbotwe and Patterson (1983) and Simbotwe (1984) in the wetlands of Lochinvar National Park, Zambia. Studies of resource partitioning among Australian lizards are those of Pianka and Pianka (1976), Pianka (1969a, 1969b), Belmont (1977), Shearer (1979), and Crome (1981). All these but the first, involve skinks.

The indices of the dispersion of a population's resource use over resource categories and the indices of morphological variation in traits related to food gathering provide different sorts of information; the first indicates the distribution of resource utilization among resource categories whereas the second indicates whether the population has phenotypes expected to differ in their average resource use. I have opted to use both. Even though it is common knowledge that over a chosen resource axis, overlap in resource utilization judged with respect to the axis may indicate competition, I have chosen not to invoke competition as an explanation. The available data are meant only to show similarities and differences in niche width or breadth and niche overlap using four resources, i.e. time, food, temperature requirements, and structural resources (see also Chapter 2, part 2). It would be necessary in addition to study many other aspects of community ecology including environmental productivity in order to link the animal niche (utilization) to interspecific competition. Recently Schoener (1977, 1982) reviewed the concept of competition and the niche and highlighted numerous problems and controversies relating to them.

MATERIAL AND METHODS

Lizards were counted hourly between 0700 and 1700 hrs over a period of two days in each month during the summer (mid November to mid February) 1981 and 1982. The object of the behavioural observations was to determine the number of hours per day lizards were active. General observations were made on escape tactics, day time and night time retreats, feeding time and resting time. These data

generated information on time niche of adult and subadult

*Lampropholis guichenoti* and adult *Hemiergis decresiensis*.

Lizard cloacal temperatures (^{o}C) were measured with a Comark multichannel electronic thermometer with a copper-constantan thermocouple probe inserted 6 mm into the cloaca of the lizard. Where lizards were found under cover, I also recorded soil temperature at the lizard's exact spot. Ambient temperature was measured five times in an hour, 1.0 m above ground in shade. Body temperature data were not used if an animal fled prior to capture; handling time prior to taking a reading was minimized. These data were used to indicate the thermal niche.

A monthly sample of frozen lizards had their stomachs removed and opened. The various foods eaten were given a common name, and classified to familial and ordinal level where possible. Prey items were identified and counted and, whole items were measured.
Prey items were also further classified according to their probable spatial location in the environment following a modification of the method of Simbotwe and Garber (1979). Arthropods in the study area were sampled using 10 pit-fall traps located in various microhabitats including fallen bark and timber, granite outcrops, shrubs and trees, as enumerated in Figure 7. Because these pit-fall traps were quarter filled with preservative, insects were removed fortnightly. Additional samples of insects were collected by hand nets.

Analytical methods

Coefficients of determination (r^{2}) were used to compare ambient and substrate temperature to body temperatures of lizards. A product moment correlation coefficient (r) was used to compare head sizes of lizards with sizes of prey eaten. An interactive χ^{2} (Sokal and Rohlf, 1969; 592) was used to

Figure 7. Physiographic features of the study site

at Newholme. Various microhabitats are

listed and explained on the map.
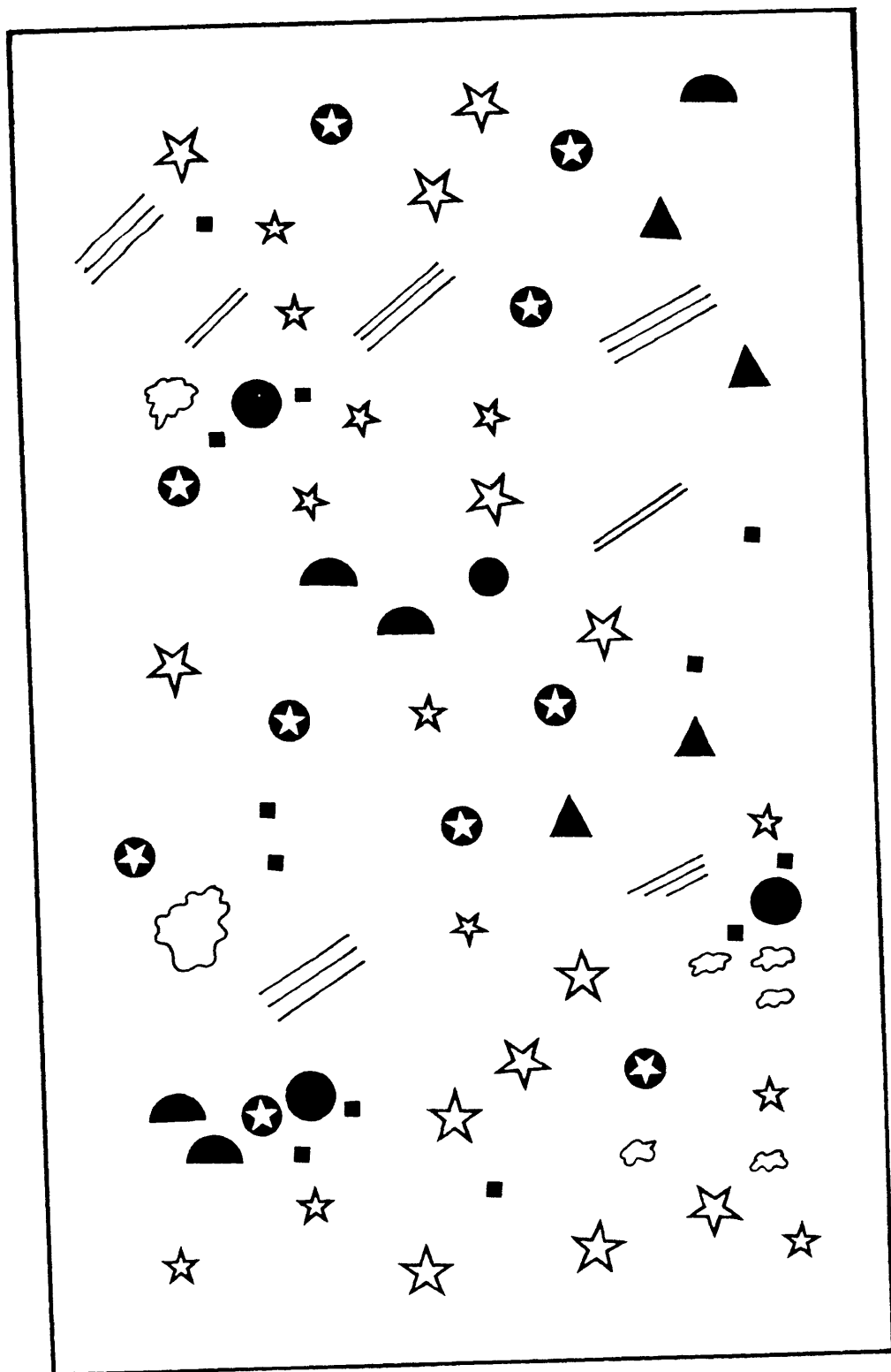
10×100m

	Trees		Tussock grass
	Fallen bark		Large tussock grass
	Granitic Outcrop		Blady grass
	Shrubs		Fallen timber
	Heath		

test the null hypothesis that both species ate the same food type
with equal frequency.

The Simpson diversity index (DS):

$$DS = \frac{(\Sigma \ P^2i)^{-1} - 1}{N - 1} \quad \text{(standardized by Levins, 1968)}$$

with values varying from 0 to 1, was used to calculate (1) time niche
breadth and (2) food niche and diversity of substrates used by the two
species.

The overlap index of Pianka (1973):

$$Ojk = \frac{\Sigma \ P_{ij} \ P_{ik}}{(\Sigma \ P^2_{ij} \ \Sigma \ P^2_{ik})^{\frac{1}{2}}}$$

was used to calculate (1) time niche overlap and (2) food niche and
place niche overlap between the two species during the summer months
of 1981 and 1982.

Because *H. decresiensis* occurred in small numbers during all the
months sampling was done, data on temperature requirements of this
species were not recorded.

Unless otherwise stated, all statistical analyses were carried
out using SPSS Batch Computer system.

RESULTS

Both the heliothermic and diurnal lizard, *Lampropholis guichenoti*
and a presumed "noctinodiurnal", thigmothermic lizard, *Hemiergis
decresiensis* were found to have similar activity patterns. Most
activity was restricted to mid-day (1000-1300 hrs). Activity started
to decrease between 1400 hours and 1500 hours with no activity recorded
after 1800 hours. The pattern was the same for subadult *L. guichenoti*.
Both air (Ta) and substrate (Ts) temperatures showed a close relation-
ship to the lizard's times of activity, with higher temperatures
recorded at the peak of lizard activity. Both lizards showed summer

Figure 8. Activity patterns of lizards of both sexes as

a function of time and temperature, A, is based

on 179 adult (closed circles) and 38 subadult

(triangles) *L. guichenoti* and B, is based on 44
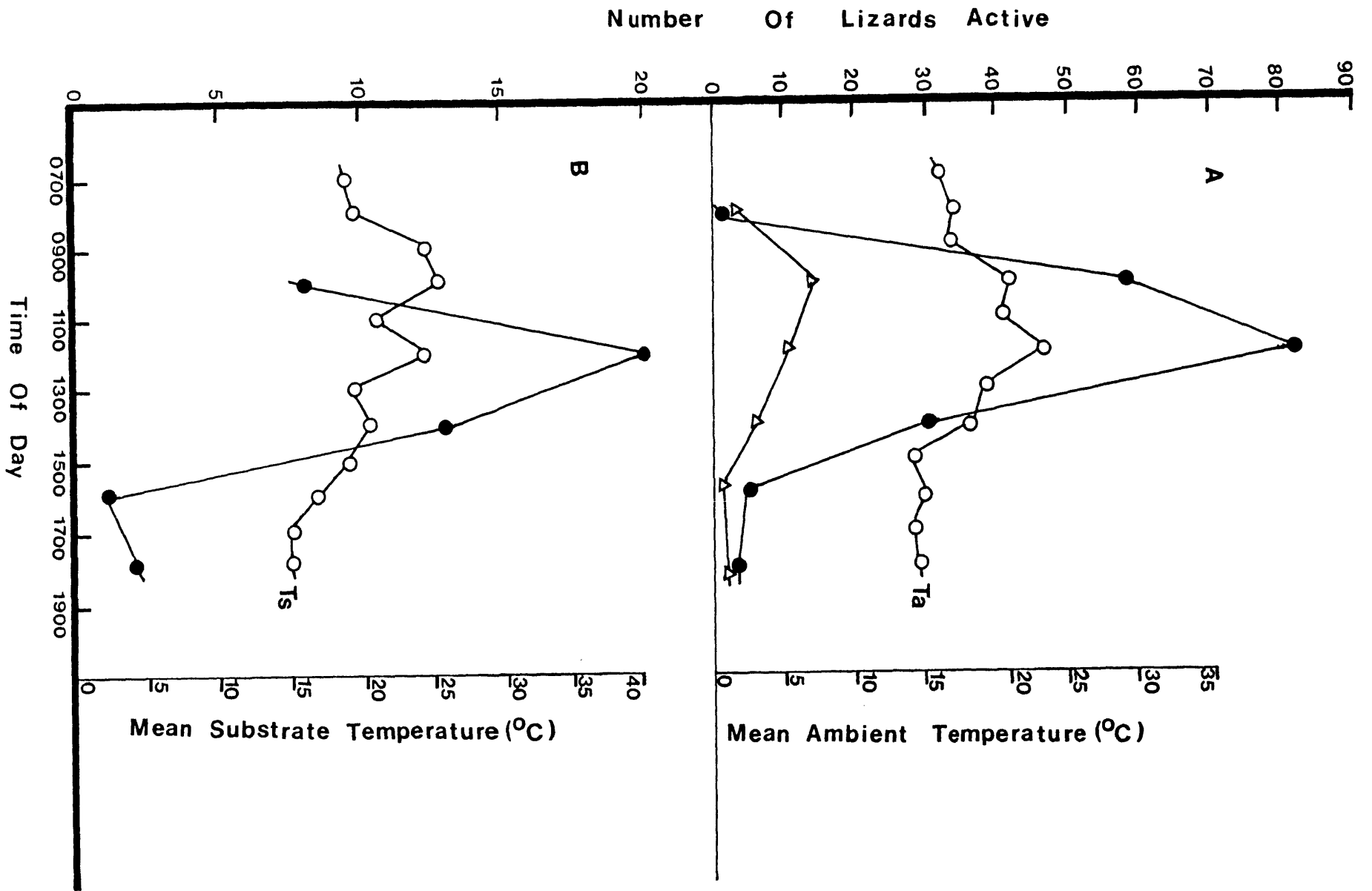
adult *H. decresiensis*.

Figure 9. Relation of cloacal temperature of *L. guichenoti*
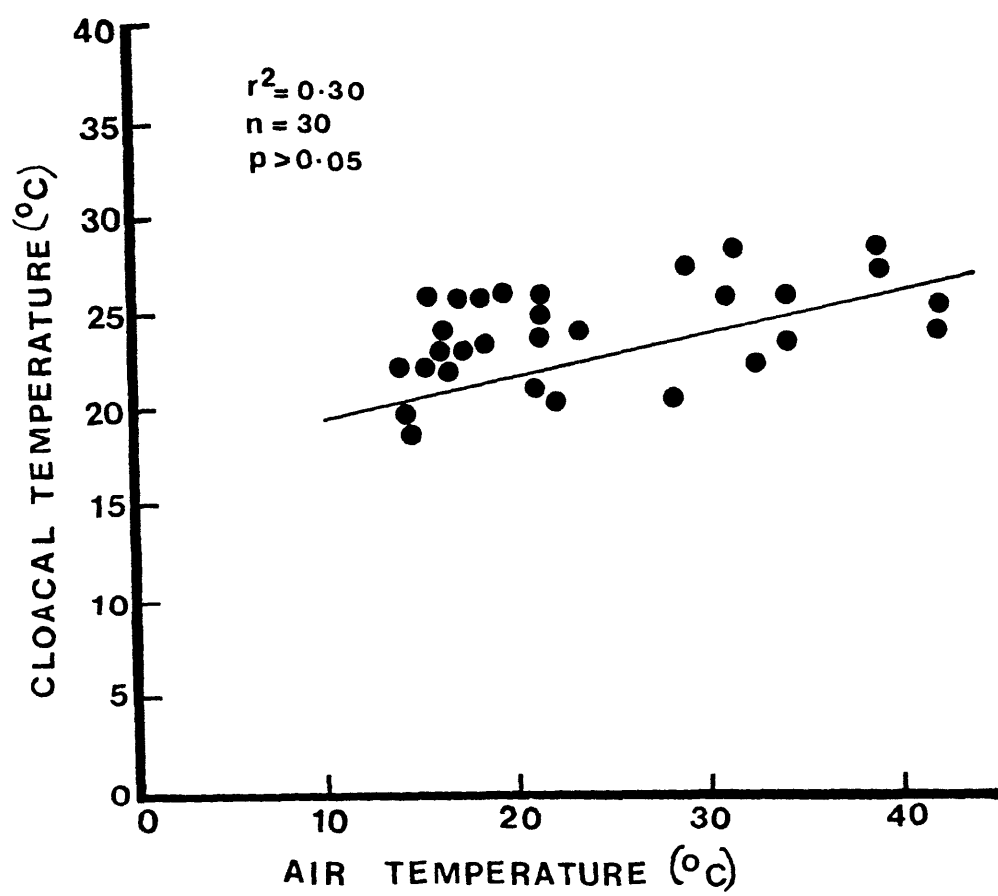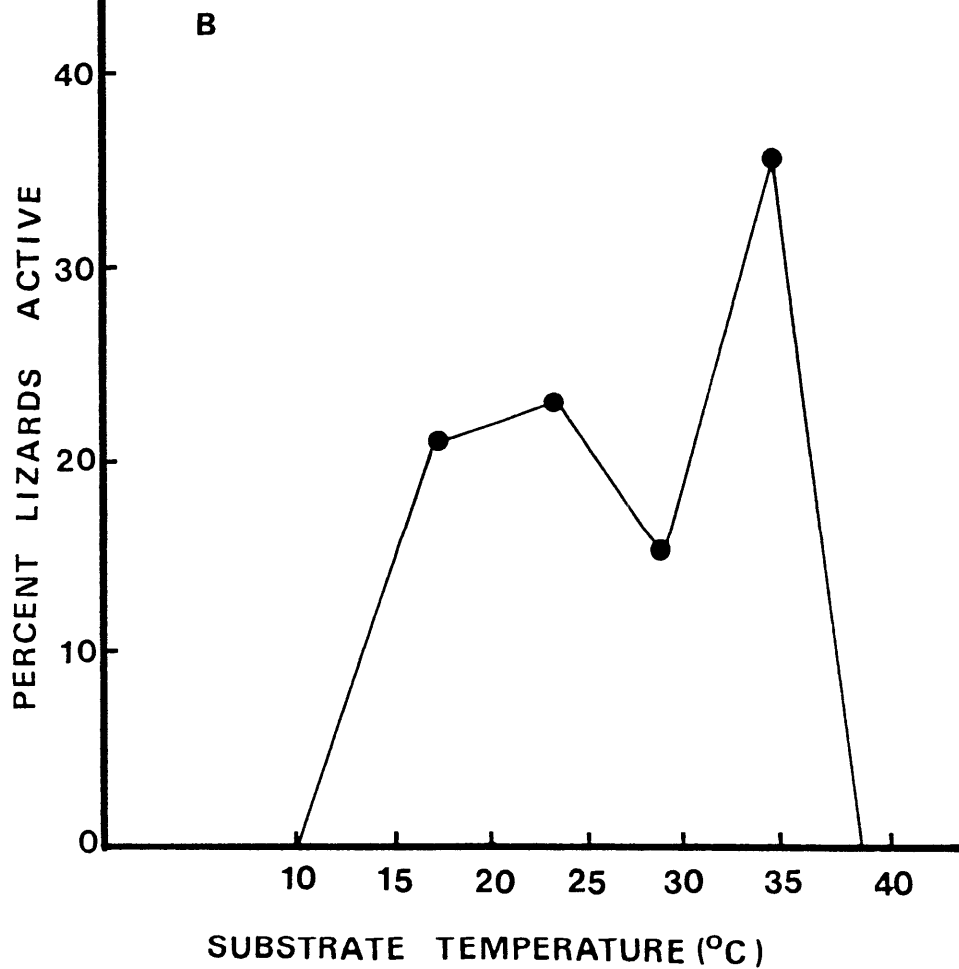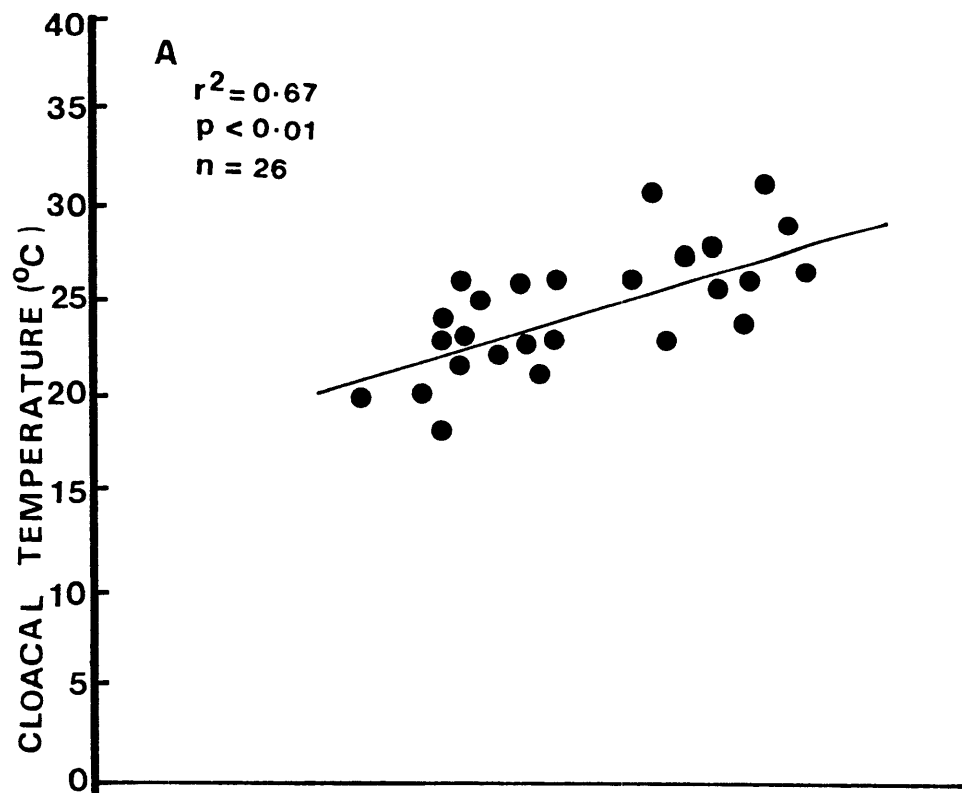
to air temperature.

Figure 10 A. Relation of cloacal temperature of

L. guichenoti to substrate temperature,

B. Relation of activity of both sexes of

L. guichenoti to substrate temperature.

bimodal activity, with peaks of activity occurring early in the day
when the environment is warming and again later when it is cooling
down (1600 to 1800 hours) (Fig. 8). *Hemiergis decresiensis* was
found to remain active an hour later in the day than *L. guichenoti*
(Fig. 8).

In *L. guichenoti*, there was a weak linear relationship between
cloacal temperature and air temperature (r^2 = 0.30, P > 0.5; n = 30
adult lizards; Y = 18.62 + 0.29x), where Y = cloacal temperature and
x = ambient temperature (Fig. 9). By contrast, there was a strong
statistically significant relationship between cloacal temperature
and substrate temperature (r^2 = 0.67, P < 0.01; n = 26 lizards; Y =
0.32x + 16.54, where Y = cloacal temperature and x = substrate
temperature (Fig. 10A). Also, number of active individuals of *L.*
guichenoti increased with increase in substrate temperature (Fig. 10B).
In adult *L. guichenoti* average body temperature in the field was
23.98°C (± SD, 2.77; n = 30) when substrate temperature ranged from
18.9° to 39.0°C ($\bar{x}$ = 27.53 ± 6.39) and air temperature was 18.37 ±
2.88°C. During the summer months, cloacal temperature ranged between
18.1° and 31.0°C. Body temperatures of *L. guichenoti* were about 18.0°C
at morning emmergence, but quickly rose to between 20° and 31°C during
the day.

Time niche breadth (DS) for *L. guichenoti* was 0.406 whereas *H.*
decresiensis had a value of 0.337. Activity time niche overlap (Ojk)
between the two species was 0.908.

The largest number of arthropods eaten were beetles, (21.95%)
and these were found in 18 stomachs (Table 2). The second most
important food for *L. guichenoti* was spiders, which comprised 17.10%
of the total food items eaten; they were represented in 14 stomachs.
Lepidopteran larvae, and flies (8.54% each) and ants which formed
7.31% of the diet (see Table 2) were some of the most

TABLE 2. Major prey items in the stomachs of two species of lizards during the summers of 1981 and 1982. Probable microhabitats of prey described by: GGL = Ground within grass and litter; GW = Ground within wood or fallen timber; AGS = Above ground among grasses and shrubs.

Prey items	L. guichenoti			H. decresiensis		
	No of prey items	No of stomachs with prey	Percent composition by number of stomachs with prey	No of prey items	No of stomachs with prey	Percent composition by number of stomachs with prey
Spiders (GGL + AGS)	15	14	17.10	3	1	2.94
Arachnidae larvae (GGL)	1	1	1.21	-	-	-
Ants (GGL + GW)	18	6	7.31	19	5	14.71
Termites (GW)	15	1	1.21	20	8	23.53
Beetles (GGL)	37	18	21.95	10	7	20.59
Coleopteran larvae (GW)	3	4	4.90	2	2	5.88
Grasshoppers (GGL)	5	3	3.66	1	1	2.94
Moths (GGL)	2	1	1.21	-	-	-
Lepidopteran larvae (GGL)	7	7	8.54	9	6	17.65
Snails (GW)	6	4	4.94	2	1	2.94
Praying mantis (GGL)	2	1	1.21	-	-	-
Dragonfly (GGL)	1	1	1.21	-	-	-
Odonata larvae (GW)	1	1	1.21	-	-	-
Dipteran flies (AGS)	12	7	8.54	-	-	-
Scorpion-flies (AGS)	1	1	1.21	-	-	-
Caddis-flies (AGS)	3	2	2.44	-	-	-
Bugs (GW)	3	2	2.44	1	1	2.94
Bees (AGS)	1	1	1.21	-	-	-
Unidentifiable insect remains	11	7	8.54	4	2	5.88
Total number of items	144	82	100.00	71	34	100.00
Food niche breadths		0.445			0.251	
Food niche overlap O_{jk}				0.749		

TABLE 3. Arthropods collected from the study area (adults plus larvae) during the summers of 1981 and 1982.

Prey items	No. of individuals	Percent composition
Spiders	36	6.47
Wolf spiders*	4	0.72
Ants	198	35.61
Termites	6	1.08
Beetles	226	40.65
Grasshoppers	4	0.72
Moths	6	1.10
Lepidopteran larvae	3	0.54
Snails	7	1.26
Praying mantis	2	0.36
Dragonfly	2	0.36
Dipteran flies	2	0.36
Scorpion-flies	3	0.54
Caddis-flies	10	1.79
Bugs	6	1.10
Bees	4	0.72
Millipedes*	7	1.26
Scorpions*	3	0.54
Crickets*	10	1.79
Leaf hoppers*	3	0.54
Centipedes*	3	0.54
Total	545	100.00

* Not recorded in lizard stomachs but present in study area.

Figure 11. Relative abundance of the principal groups

of arthropods eaten by *L. guichenoti* and
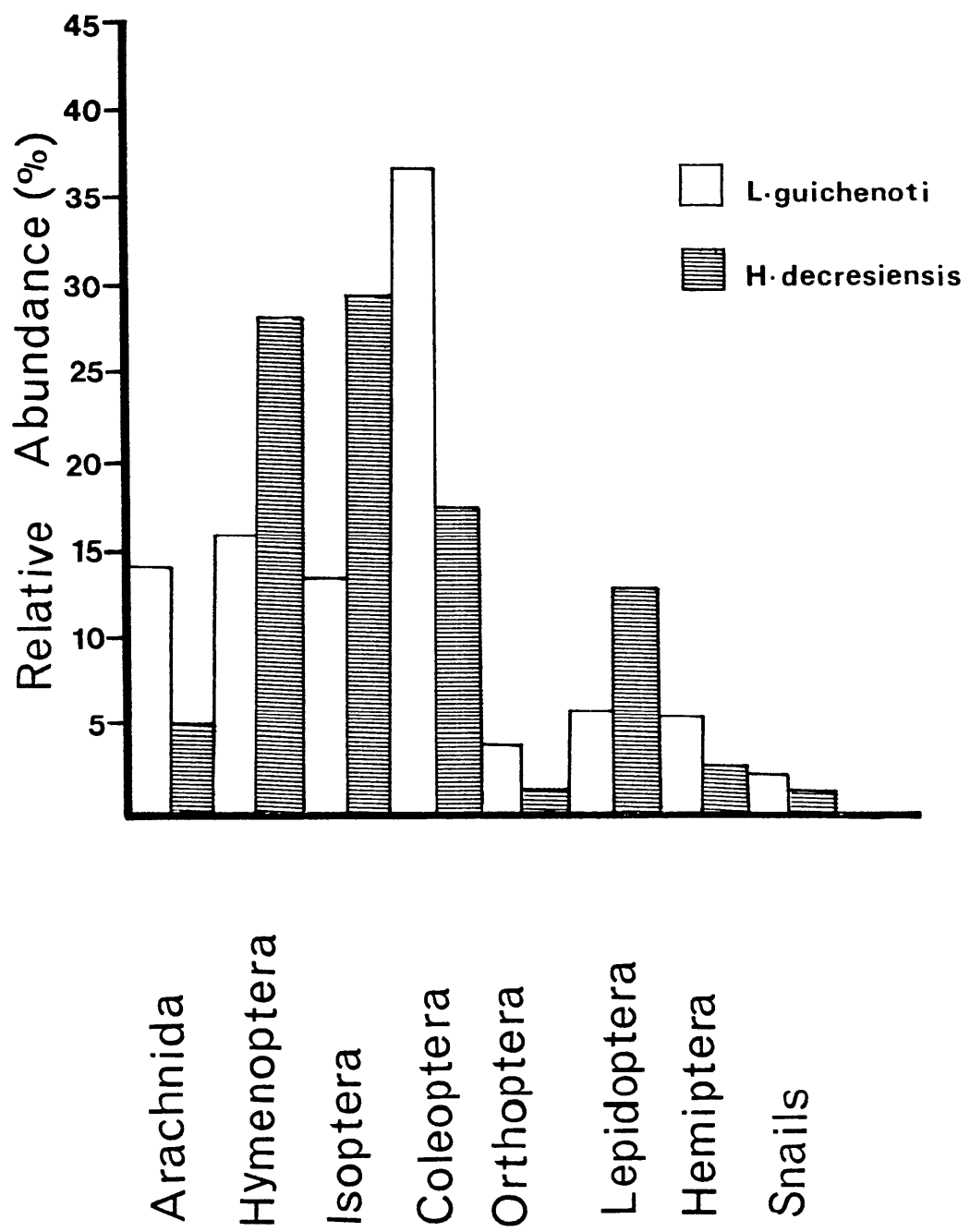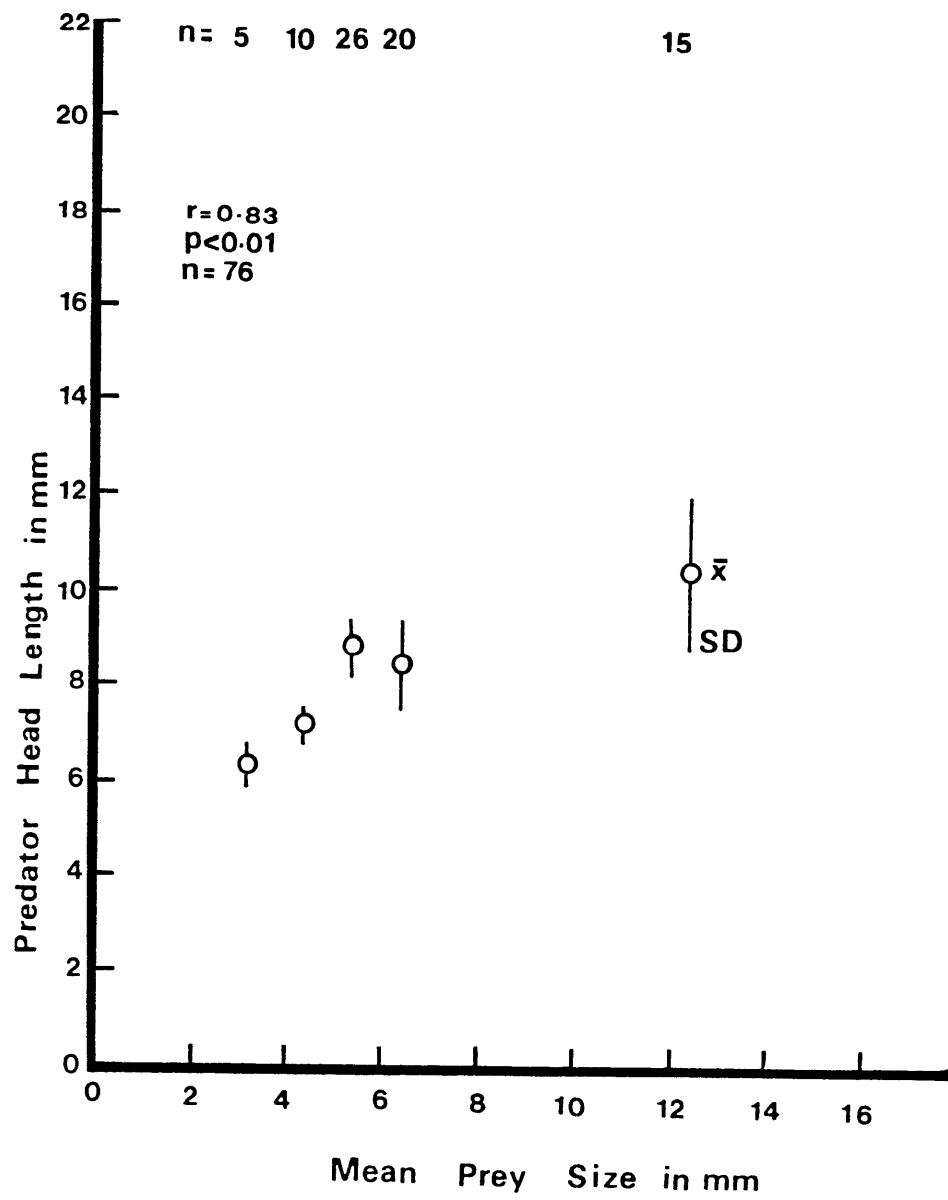
H. decresiensis.

Figure 12. Relationship of predator head size to size of

food eaten by female *L. guichenoti*.

important food items eaten by *L. guichenoti* during the summer months. Table 2 also lists the total number of prey items in each of the 19 categories and the percentage occurrence by number of each prey type.

The most important food for *H. decresiensis* during summer was termites. They made up 23.53% of the total food items in the stomachs and were represented in 8 out of 34 stomachs examined. Ants (14.71%), lepidopteran larvae (17.65%) and beetles (20.59%) also comprised a significant part of the diet. Figure 11 shows food taken by both species and the frequency with which each food item was eaten by respective species. A G test retained the null hypothesis that there were no differences in the frequencies with which the two species ate different food items (P > 0.99). That they actually did eat the foods with equal frequency also is supported by a large food niche overlap value (Ojk = 0.749) (Table 2). Figure 11 also shows the relative abundances of the principal groups of arthropods taken by the two species. Hymenopterans, isopterans, coleopterans and lepidopterans stand out as the most utilized foods by both species.

Table 3 gives a list of arthropods collected from the study area during the summer months. Six arthropods were present in the study area, but not eaten. These included centipedes, crickets, leaf-hoppers, millipedes, scorpions and wolf spiders (Table 3).

Correlation of body size (SVL) to head size (HL) showed a significant linear relationship in males (r = 0.902, P < 0.01, df = 91) and females (r = 0.906, P < 0.01, df = 90) of *L. guichenoti*. Head lengths of female *L. guichenoti* showed a highly significant statistical relationship with mean prey size (r = 0.83, P < 0.01, df = 74) (Fig. 12).

Food niche breadth was 0.445 for *L. guichenoti* and 0.251 for *H. decresiensis* (see also Table 2).

DISCUSSION

Lizards' pattern of activity may be closely linked to time because the latter has strong influence on both air and substrate temperatures (for example, see, Pianka, 1969a). In this study, both air and substrate temperatures were strongly time-dependent, a result that supports Pianka's (1969a) statement that "a lizard's temporal activities must be closely geared to its thermoregulatory requirements." The influence of time and weather was demonstrated by Pianka (1969a) in an Australian scincid, *Ctenotus calurus*. This lizard shifted its activity seasonally. Among lizards that are active year round, it has been shown that those species that have a bimodal daily pattern of activity in summer (active in early morning when the environment is warming up and later in the day when the environment is cooling) undergo a seasonal shift in activity in winter and become active only at mid-day (Mayhew, 1964; Pianka, 1969a). Heatwole *et al.*, (1969) have designated such species as type I lizards and emphasized that they sacrifice length of activity period for achievement of precise thermoregulation, in contrast to type II lizards which sacrifice thermoregulatory precision for maximization of length of daily activity. Body temperatures of *L. guichenoti* showed a weak correlation with air (Ta) temperatures but were well correlated with substrate (Ts) temperatures. In fact, more lizards became active as substrate temperatures increased. *Lampropholis guichenoti* forages on the surface and retreats among bark, fallen wood, grass and ground litter. Pianka (1969a) also found that skinks that foraged in the open had body temperatures that were not highly correlated with air temperature. Both *L. guichenoti* and *H. decresiensis* showed a slight bimodal daily activity pattern. The juveniles of *L. guichenoti* showed a similar daily activity pattern, with most of their activity being confined to early morning; only

limited activity occurred later in the day. *Hemiergis decresiensis* had a slightly narrower time niche breadth than *L. guichenoti;* the latter species was active in the morning at least an hour earlier than the former. However, overlap in time of activity is very high. Firth (1968) provided an experimental laboratory study of activity in these species, which largely support present findings.

Lampropholis guichenoti forages in the open among fallen wood, litter and grasses whereas *H. decresiensis* is fossorial and slow and during the day remains active under cover within fallen wood heaps overgrown with grass and mixed with fallen leaf and bark. Individuals were heard or located among fallen rotting logs or underneath tree bark.

Any similarities and differences in diet between the two species can be accounted for largely by broad overlap in foraging and micro-habitat. Even though *L. guichenoti* shelters under objects where *H. decresiensis* spends much of its time, the former species forages in the open and catches, in addition, a variety of faster moving prey. Both of these species are generalist, opportunistic feeders taking a variety of arthropods of different types and sizes. Beetles of the family Carabidae and Staphylidae were the most common prey, with the spider families Lycosidae and Salticidae also being common prey for *L. guichenoti*. Indeed, Crome (1981) recorded these spiders to be the most common food of this lizard. Whereas Crome (1981) recorded only larvae of lepidopterans in *L. guichenoti* stomachs, the present study recorded a moth as well as larvae among the food items eaten. The listing of arthropods' probable microhabitats suggest that spiders, beetles, flies and lepidopteran larvae are located mostly where the lizards forage, i.e. amongst litter and low vegetation. It is possible that dietary differences between species may be a good indicator of temporal and structural niche differences (see Pianka, 1969a).

Termites, beetles, lepidopteran larvae and ants formed the most common prey items of *H. decresiensis*. On the contrary, Crome (1981) reported ants to comprise the bulk of the diet of *H. decresiensis* (75% of the total number of prey items eaten and contained in 78% of the stomachs examined). In Crome's (1981) study, termites formed a greater part of the diet of *L. guichenoti* than of *H. decresiensis*. This difference may reflect differences in the two study areas. The present study site suffered severe die-back and dead wood and wood termites were abundant. However, Belmont (1977) found that the main prey items of *L. guichenoti* were collembolans but none were recorded by either Crome (1981) or by the present study. Basically, all the most common prey of both species shelter in microhabitats utilized by both lizards. This could account for similarity in diet. Because *H. decresiensis* has weak limbs, is slow and forages under cover, it was not surprising that its diet is restricted compared with that of *L. guichenoti*. However, where prey items are shared in common, they are utilized in a similar manner and with equal frequency.

Hemiergis decresiensis showed shorter times of activity than *L. guichenoti*. This restricted activity period may be a result of the damp microhabitats of *H. decresiensis* which may warm much more slowly than the drier, more open microhabitats in which *L. guichenoti* forages. Firth (1968) reported that *H. decresiensis* seem to prefer lower fluctuating temperatures, with a high degree of nocturnal activity compared to diurnal activity. This restriction of activity and foraging ability of *H. decresiensis* may be related to its narrow microhabitat niche and more restricted diet compared with *L. guichenoti*.

Time of day was found to influence air and substrate temperatures greatly, and diel activity was found to be closely geared to all these factors.

PART 2

CHAPTER 2

HABITAT USE

INTRODUCTION

Detailed studies of habitat selection and use and of habitat specificity include those of Pianka (1969a, 1969b), and Heatwole (1977). Central to these studies is the idea that in more heterogeneous environments, lizards may recognize more habitats through learned behaviour or adaptation to specific physical environments. These aspects in turn allow coexistence through partitioning of available microhabitats among various species (Pianka, 1969a, Heatwole, 1977). Schoener (1977: 115) discussed general aspects of reptilian niches in relation to interspecific competition.

Even though Pianka (1969a, 1969b) mentions habitat partitioning in scincids (*Ctenotus*), the only detailed study of substrate selection in scincids has been that of Huey and Pianka (1974) and Huey *et al.* (1974). Animals are known to possess two types of habitat space, home ranges and territories. Only the latter is defended. The only study of movements in Australian lygosomine skinks is by Milton (1980).

The present study aims to elucidate habitat use by *Lampropholis guichenoti* and *Hemiergis decresiensis* in the Newholme area, N.S.W., and to describe movements of the former species.

MATERIAL AND METHODS

For each lizard seen, species, microhabitat and substrate were recorded. Four microhabitats were recognized: (1) open ground, (2) ground with grasses and litter, (3) fallen wood and (4) rock piles.

Features of the habitat are given in figure 7, Chapter 2, Part 1.

Individuals of *L. guichenoti* were toe-clipped using the technique of

Tinkle (1967). *H. decresiensis* has small, weak limbs and toes which

made toe-clipping difficult, and occurred in small numbers at all

seasons during marking; accordingly, this species was not toe-clipped.

For both species, body size (SVL), body weight (g) and tail length and

tail morphology (broken, regenerated or original) were recorded. They

were then toe-clipped (*L. guichenoti*) and later released at the point

of capture where numbered stakes were placed following capture or re-

capture in order to be able to follow the animal's movements over a

period of time.

Statistical analysis

Simpson's diversity index (DS) standardized by Levins (1968) and

the overlap index (Ojk) of Pianka (1973) were used to calculate diversity

of substrates used by both species and structural niche overlap between

the two species (for details relating to the formulae, see Part 1,

Chapter 2). An interactive χ^2 (Sokal and Rohlf, 1969: 529) was used to

test the null hypothesis that there was no difference in the frequency

with which the two species utilized available microhabitats.

For convenience, the hectare where movement studies were carried

out was marked into 10 transects, each 0.1 ha.

Natural predators that had overlapping activity periods with the

lizards were recorded and lizards were examined for external indication

of parasitic worms following the methods of Daniels and Simbotwe (1984)

(Appendix 3).

RESULTS

Lampropholis guichenoti is a diurnal lizard found active among fallen wood, grasses, bark and leaf litter, whereas *H. decresiensis* is fossorial and was found active under cover during the day, within fallen wood and ground litter. As a result of die-back, most trees had bark heaped at the tree base and these areas were popular day time and night time retreats for both lizards. These lizards shelter communally either in single species congregations or as mixed species aggregation composed of *H. decresiensis, L. guichenoti* and *Lampropholis delicata*. Most lizards carried cystacanths of the helminth, *Sphaer-echinorhynchus rotundocapitatus*.

Two likely predators of these small skinks were recorded in the study area, *Pseudechis prophyriacus* and *Pseudonaja textilis*.

Lampropholis guichenoti uses a greater variety of substrates (structural niche diversity 0.624) than *H. decresiensis* (DS only 0.492). Structural niche overlap was 0.481 and was lower than for either time or food niches. Table 4 shows the relative occurrence of these species and the diversity of microhabitats they used. A chi-square test of independence (G = 14.14, P < 0.005, df = 2) led to rejection of the null hypothesis that there was no difference between the two species in the frequency with which they utilized microhabitats, i.e. the two species actually selected microhabitats with different frequencies.

Eighty-six lizards (subadults and adults) were marked and released in the summers of 1982 and 1983 and of these, 8(9.3%) were recovered and 5(5.8%) of them recaptured twice after the initial capture and marking. Seventy-eight animals (90.7%) were never recaptured. Among

TABLE 4. Relative occurrences of *L. guichenoti* and *H. decresiensis*
in various microhabitats and on various substrates.
Sample sizes are given in parentheses.

Microhabitats	Species			
	L. guichenoti		*H. decresiensis*	
Ground - open	(81)	0.395		-
Ground within grasses and litter	(80)	0.390	(10)	0.185
Fallen wood	(41)	0.200	(30)	0.556
Rock piles	(3)	0.015	(14)	0.259
Microhabitat niche breadth	0.624			0.481
Microhabitat niche overlap		0_{jk}, 0.492		

Figure 13. Movement of individual *L. guichenoti*.

The arrows indicate the net direction moved

between captures while numbers refer to the

number of the stake used as a marker.

100

100 m
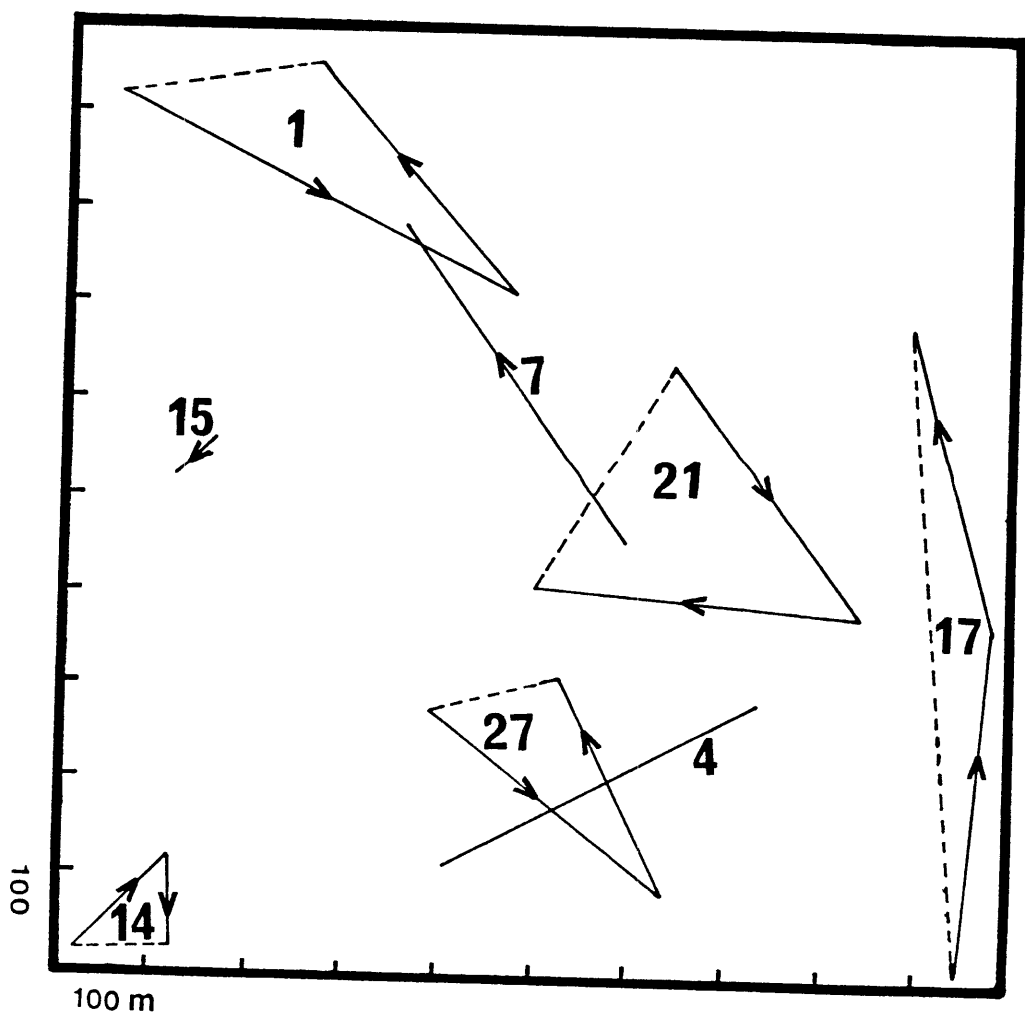
recaptured individuals was included a hatchling which had moved at
least 10 m since marking. Adults were found to have moved a minimum
of 37 m (see also Fig. 13). Only one individual marked in 1982 was
recovered in the spring of 1983, indicating a high population turn-over
rate.

DISCUSSION

The most important aspects of time, food and space lie in the
assessment of the relative significance of these factors to the species
studied and verification of how close or distant the two lizards are
in resource requirements. *Lampropholis guichenoti* is basically a
ground dweller and forages in the open and on the ground where there
are grasses and litter; 78.5% of the individuals were recorded from
such microhabitats, with 20% recorded on fallen wood, and 1.5% on rock
piles. *Hemiergis decresiensis* was most frequently recorded underneath
fallen wood (55.6%) but with 25.9% under rock piles and 18.5% on the
ground in grass and litter. These results agree with those of Cogger
(1975), Pengilley (1972) and Shearer (1979) on *Leiolopisma guichenoti*
and *H. decresiensis*.

I have shown that *Lampropholis guichenoti* has niche breadths
varying between 0.44 and 0.62 whereas those of *H. decresiensis* were
between 0.25 and 0.48. This reveals that *H. decresiensis* was rela-
tively limited with respect to the spectrum of resources used. It
was most limited in terms of varieties of foods eaten and time of
activity   but less so in terms of varieties of microhabitats used.
The possible reasons for this are given in Part 1 of Chapter 2.
Similarity in the sorts of resources utilized by both species may lead
to interspecific competition. Hence these two species were most

similar only in the times of activity and foods eaten. Because

H. decresiensis does not venture far from cover (see also comments

in Shearer, 1979), these two lizards were found to be most dissimilar

in the use of space resources.

Keast (1959) suggested that the distribution of ground skinks does

not depend greatly on the floristic characteristics of the habitat,

but that structure and degree of "openness" of the vegetation is

important. Newholme is open, a microhabitat which *L. guichenoti* seems

to prefer (Belmont, 1977; Milton, 1980).

MacArthur and Levins (1967) were the earliest to develop the

theoretical basis for relationship between niche overlap and niche

breadth. They also characterized these aspects of niche dimensionality

and related them to environmental heterogeneity (grain) and environ-

mental uncertainty. Levins (1968) developed the theory much further,

and it has now developed to such an extent that today's "... ecological

theory about species diversity begins with the niche widths as given

parameters" (Roughgarden, 1974).

The present study recorded distances covered by *L. guichenoti*

ranging from 10 to 37 metres. Shearer (1979) calculated distances

covered in several species of skinks he studied including *Leiolopisma*

guichenoti and *H. decresiensis*. He recorded distances of from 6 to

110 metres in the former species. But Milton (1980) gave a standard

deviation of 29.3 m and suggested that "given the large distances

moved within the study area, there may be a continual movement into

and out of the study area." The small distances moved by these lizards

seem to be typical of lizards in general. Fitch's (1973a) field study

of Costa Rican lizards recorded in most species marked individuals that

were recaptured after an interval of a month or more to have moved no

more than 15 metres. Typical home ranges of most lizards had radii

of 5 to 12 metres.

Both species studied exhibited no territorial behaviour, but certainly have home ranges, i.e. areas they frequently visit and live in. Like *L. guichenoti, Eumeces fasciatus* is not territorial (Fitch, 1954); both *H. decresiensis* and *E. fasciatus* are secretive and never venture out of cover even when foraging (see Stamps, 1977a). For a discussion on territory and home range defense refer to a review paper by Stamps (1977a) and the literature cited therein. Some workers believe that the non-occurrence of territorial behaviour in the majority of skinks may be a result of their being low to the ground with a consequent obstruction to distant vision (Bustard, 1970b; Stamps, 1977a).

CHAPTER 3

MORPHOLOGY

PART 1

CHAPTER 3

GROWTH

INTRODUCTION

Studies addressing the problem of individual growth rates

of lizards in nature are few and mostly based on temperate species

(Blair,   1960; Gibbons, 1968; Clark, 1970; Gibbons, 1972; Wilbur,

1975; Kaufman *et al.*, 1975; Ballinger *et al.*, 1980). Detailed

studies of growth rates in scincids are anecdotal and in most cases

do not address the sorts of problems or data reviewed recently by

Andrews (1982).

Reptilian growth patterns resemble step functions and growth

tends to cease at scenescence (Andrews, 1982). Contrary to the reports

by Blair (1960) and Iverson (1979) reptilian growth does not show a

monotonic increase. The basic approach to studies of reptilian

growth patterns has been twofold: (1) studies of prenatal growth

and (2) studies that deal with postnatal growth, i.e. starting at

birth or hatching. Literature on growth rates in reptilian embryos

is summarized in detail by Andrews (1982). Most such studies show

that growth rates of embryos are greater than those of neonates

(Brody, 1945; Ricklefs and Cullen, 1973). Interpretation of growth

rate differences in reptiles have roots in the recent development

and popularization of optimizing ecology. As a consequence, growth

has naturally been accepted as one of the three major life history

components along with maintenance and reproduction. Gadgil and

Bossert (1970) have used these components as the bases upon which

time-energy budgets are divided in maximizing fitness. Hence the

basic difference in growth rates among species must lie in differ-

ences of life history phenomena which demand different energy

allocation at different stages of the life cycle. For example,

embryos thrive on protein-rich food (yolk) and need energy to support

only growth maintenance. Hatchlings, on low energy food (Andrews,

1982: 275) must in addition, move and look for food, capture and eat

it, escape predators, seek shelter, fight intruders and face intra-

specific and interspecific competition. All these activities, including

growth, demand an expensive energy support system. Individual growth

rates in *L. guichenoti* hatchlings is high but this slows after sexual

maturity (Heatwole, 1976). This pattern is true for other reptiles

(Blair, 1960; Gibbons, 1968; Clark, 1970; Wilbur, 1975). In the diurnal

gecko, *Lygodactylus chobiensis,* the relationship between weight and

length tended to be curvilinear among sexually immature individuals.

However, with the exclusion of this group, the relationship became

linear and in the form: $Y = 19.6 + 0.97x$ (Simbotwe, 1983a). Similarly,

Kaufman *et al.* (1975) in a study of *Crotalus horridus* adults came to

the conclusion that the relationship of body weight and length among

mature individuals is linear. This relationship can be used to predict

metabolic rates in reptiles since growth in reptiles is found to be

related to body mass by nearly the same power as are metabolic rates

(see Andrews, 1982 for details). Two methods of plotting growth curves

have been employed: (1) the first and by far the simplest is the

method in which straight lines are drawn between points, the points

representing the size of individuals on successive recapture dates,

(2) the Von Bertalanffy model (see Turner and Gist, 1970; Pengilley,

1972; Trivers, 1976; Dunham, 1978; Schoener and Schoener, 1978; Van

CHAPTER 2

NICHE RELATIONS

CHAPTER 3

MORPHOLOGY

CHAPTER 4

FEMALE REPRODUCTIVE CYCLE

CHAPTER 5

MALE REPRODUCTIVE CYCLES

Devender, 1978 and Chabreck and Joanen, 1979). I opted to use
the first method because of its simplicity and clarity.

High variability in growth rates is characteristic of
reptiles. Both intrinsic and extrinsic factors are involved in
bringing about this variability. Among temperate reptiles, growth
is either minimal or ceases in winter. Maximal growth rates
are attained during the summer (Pengilley, 1972). In the tropics
reptilian growth patterns reflect different seasons with unequal
lengths and showing much variability in temperature, total hours of
activity and duration of insolation and rainfall. Pilorge and
Castanet (1981) developed a technique using skeletochronological
methods taking advantage of discontinuous tissue growth in temperate
reptiles during the winter. This method, in addition to capture-
mark-recapture techniques has provided a more precise means of
determining age-specific demographic structure (Pilorge, 1982).
Using individuals of known ages of the lizard *Lacerta vivipara*,
Pilorge (1982) showed discontinuous growth patterns during successive
winters from birth to death. Like many others (Andrews, 1982
and lit. cit. therein) he found that growth rates slow down con-
siderably at sexual maturity, are minimal at 2 years of age and
nil among individuals in their fourth winter of brumation. This is
in contradiction to the common belief that reptiles continue to
grow throughout life (Porter, 1972). The important factors deter-
mining growth rates in reptiles include circannual rhythms of
appetite, food and water availability, temperature, number of hours
of sunlight (Licht, 1972, 1974; Blair, 1960; Tinkle, 1967; Medica
et al., 1975; Stamps and Tanaka, 1981; Harlow *et al.*, 1976; Harwood
1979 and Moll and Legler, 1971) and availability of prey (Andrews,
1971; Trivers, 1976 and Stamps, 1977b).

The social environment also has been suggested as affecting

individual growth rates (see Rand, 1967; Berry, 1974, and Froese

and Burghardt, 1974). Various workers have shown a significant

reduction in body growth following tail loss in the juveniles of

many lizards (Congdon *et al.*, 1974; Vitt *et al.*, 1977; Ballinger

and Tinkle, 1979). Growth also may vary according to sex (Pengilley,

1972). In general, growth differences parallel sexual differences

in adult body size (Pilorge, 1982). Despite all the empirical

and laboratory methods that have involved manipulation and control

of certain factors, many authors have worked with animals whose age

could not be determined precisely even by skeletochronological

techniques (Bradshaw, 1981). Short-term and long-term weather

information of localities where studies are carried out are often

lacking and where it is available, it does not permit calculating

predictability, constancy and contigency in the cyclic factors of

temperature, humidity, rainfall and insolation. This information

is important in learning about environmental cues and developmental

timing in lizards.

The role of predation in natural regulation of animal numbers

and its indirect effects on the amount of energy available to the

population is not well understood, mainly because predation is rarely

observed in the field and because of difficulties in interpretation

of predation pressure from results on tail loss and tail regeneration

(Pilorge, 1982). It is necessary to know the diet and energy re-

quirements of predators (Simbotwe 1983b). It is also necessary

to estimate quantitatively the resources available to the population, and

the effects of competition for food (Pilorge, 1982).

The other causal factor which in future may be found to affect

the general health of reptiles and which could be manifest in their

growth and behaviour is parasitism (see comments in Simbotwe, 1979 and Simbotwe, 1983c). A pathologic condition or mere high levels of parasitism could result in loss of condition which may in turn cause loss of appetite, and reduced growth. Even though very few herpetologists ever consider parasitism, helminth parasitism is part of the life of many reptiles. Daniels and Simbotwe (1984) reported high levels of infestation by Acanthocephalan crystacanths in *Hermiergis decresiensis* which resulted in emaciation of the host (see Appendix 3).

The genetic basis of reptilian growth also is not well understood. Transplantation experiments of individuals from the same population to different geographic regions may reveal taxonomically and related lineage-specific growth patterns and may reveal the extent of control of growth early in the genome. However, Burrage (1973) showed that in *Chamaeleo namaquensis*, sexual differences in growth rates vary geographically.

The cyclic nature of wet and dry seasons, temperature, insect availability, length of hours of sunlight, and activity periods, including density dependent and density independent control of animal numbers and the nature of spreading risk must all be well understood (see also Den Boer, 1968).

Apart from a mention of growth in the scincid *Typhlosaurus lineatus* by Huey *et al.*, (1974), and Pengilley's (1972) work on several lygosomine skinks from Coree flats, N.S.W., Australia, there are no studies of growth rates in skinks. In Australian lizards growth has been studied in three agamids, *Amphibolurus fordi* (Cogger, 1969), *Amphibolurus ornatus* (Bradshaw, 1981) and *Amphibolurus minor* (Davidge, 1979).

The present study presents snout-vent length frequency distribution of *Lampropholis guichenoti* and *Hemiergis decresiensis* and shows patterns of growth by individuals captured at different monthly intervals during spring, summer and autumn.

MATERIAL AND METHODS

Lizards were collected at monthly intervals and their snout-vent length (SVL) measured by vernier calipers to the nearest 0.1 mm. Lizards were sexed in the field by palpation of the base of the tail to stimulate eversion of the hemipenes (Simbotwe, 1983b). In 96.6% of the cases the individuals subjected to palpation but which did not evert the hemipenes, were actually females, as verified through killing of 30 palpated specimens and sexing them by examination of the gonads. Thus the technique has only a 4% error in favour of females. Sexed lizards, plus unsexed hatchlings of *L. guichenoti* were marked and released at the point of capture. *Hemiergis decresiensis* could not be marked by a toe-clipping technique because it has small, weak limbs and toes. Growth rates in *L. guichenoti* were determined by dividing the number of days between successive recaptures into the difference in snout-vent length (SVL) of an individual lizard. Recaptures at intervals of less than one month were excluded in order to standardize the procedure and minimize measurement error (see Ballinger and Congdon, 1980).

In the winters of 1981 and 1982, the study area was visited at least once a week to see if any animals would emerge from hibernation on warm, sunny days. None was ever observed.

Specimens of *Lampropholis guichenoti* used in reproductive studies were sexed and placed in the following size groups:

Stage 1. Hatchlings (20.8 mm SVL), subadult males (20.9-27.1 mm SVL) and subadult females (20.9-26.4 mm SVL). These groups are immature and under 1 year of age.

Stage 2. Adults in their first year of reproductive life included males (27.2-36.8 mm SVL) and females (26.5-36.8 mm SVL).

Stage 3. Adults in their second year of reproductive activity included males and females of 36.9-38.8 mm SVL.

Stage 4. Adults with more than 2 years of sexually active life included males (38.9-43.0 mm SVL) and females (38.9-46.0 mm SVL).

Catergorization and ageing of various body size (SVL) groups are based on data from capture-mark-recapture programme.

RESULTS

Some indication of growth can be gleaned from size class information during different months (Figs. 14 and 15). Hatchlings (individuals with umbilical scars) of *L. guichenoti* range from 14.0-20.5mm (SVL) ($\bar{x}$ = 18.8 ± 0.85 SD, N = 30) and from 0.10-0.21 g ($\bar{x}$ = 0.13 ± 0.05, n = 19) in body weight. *Hemiergis decresiensis* hatchlings have body sizes (SVL) ranging from 20.6 to 29.91 mm ($\bar{x}$ = 27.5 ± 5.25, n = 17) and from 0.12 to 0.48 g ($\bar{x}$ = 0.35 ± 0.20, n = 17 in body weight.

Lampropholis guichenoti hatchlings appear in February and are in great abundance. As many as 15 per 400 m^2 or 375 hatchlings per hectare were recorded. Hatchlings were observed feeding during most of the activity period. They are active and grow for four months before their first winter brumation. By the time they enter the winter inactivity period, their umbilical scars have healed and they measure between 21 and 25 mm SVL (Fig. 14). When they emerge in spring, some juvenile *L. guichenoti* are still between 23.0 and 25.8 mm SVL (Fig. 14).

Newborn of *H. decresiensis* appear in December. A one day old animal born in December in a collector's bag measured 20.6 mm SVL. Newborn were rarely encountered, and when collected appeared distended. They grow about 5 months before their first winter brumation. They enter the winter inactivity period at a minimum size of 25 mm SVL and at this

Figure 14. Monthly abundances of different-sized

L. guichenoti. The arrow denotes a growth trend

for a cohort of juveniles. Each solid circle

equals one individual (N = 268). The winter
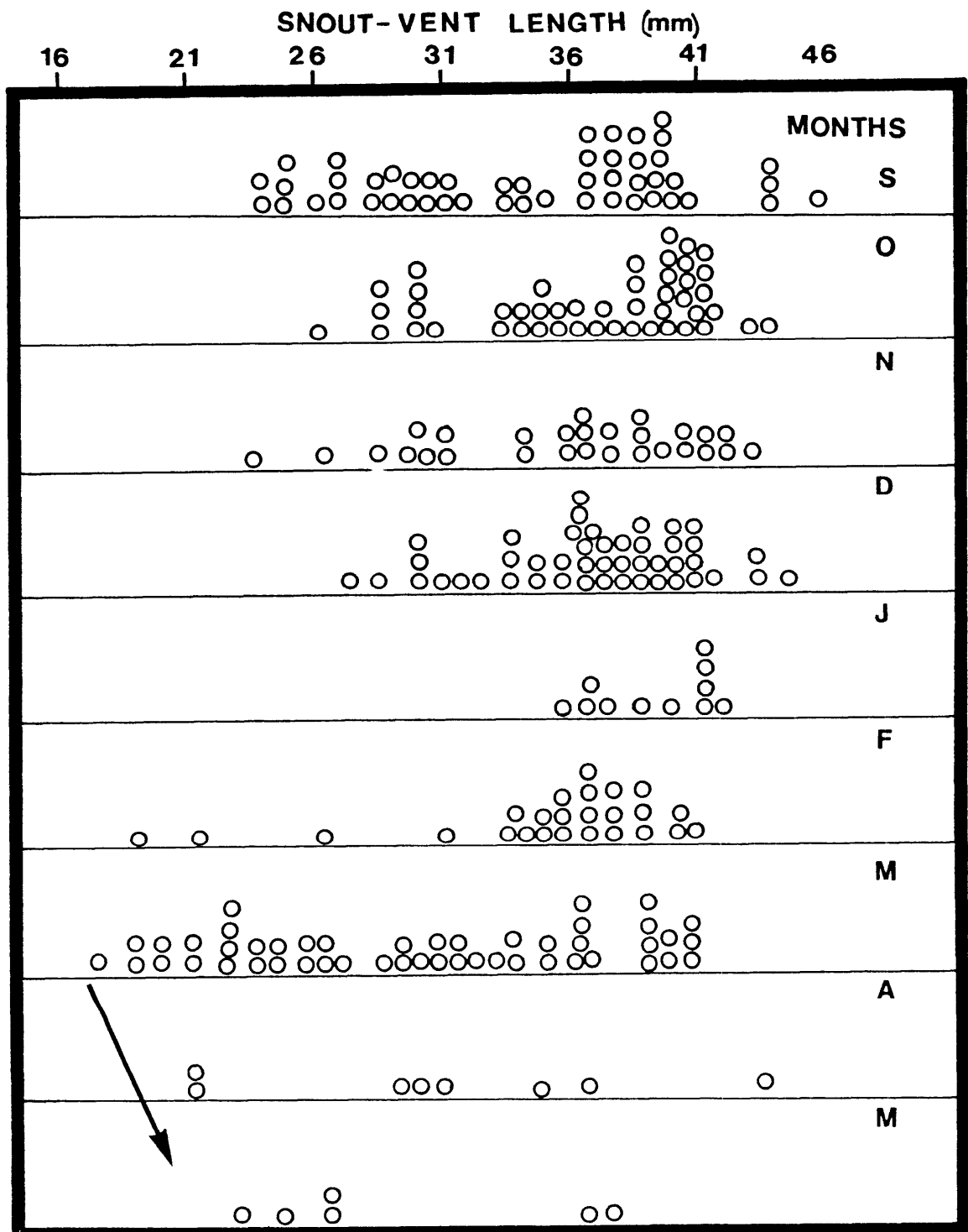
inactivity period is June to August.

SNOUT-VENT LENGTH (mm)

Figure 15. Monthly abundances of different-sized

H. decresiensis. See Fig. 14 for explanation
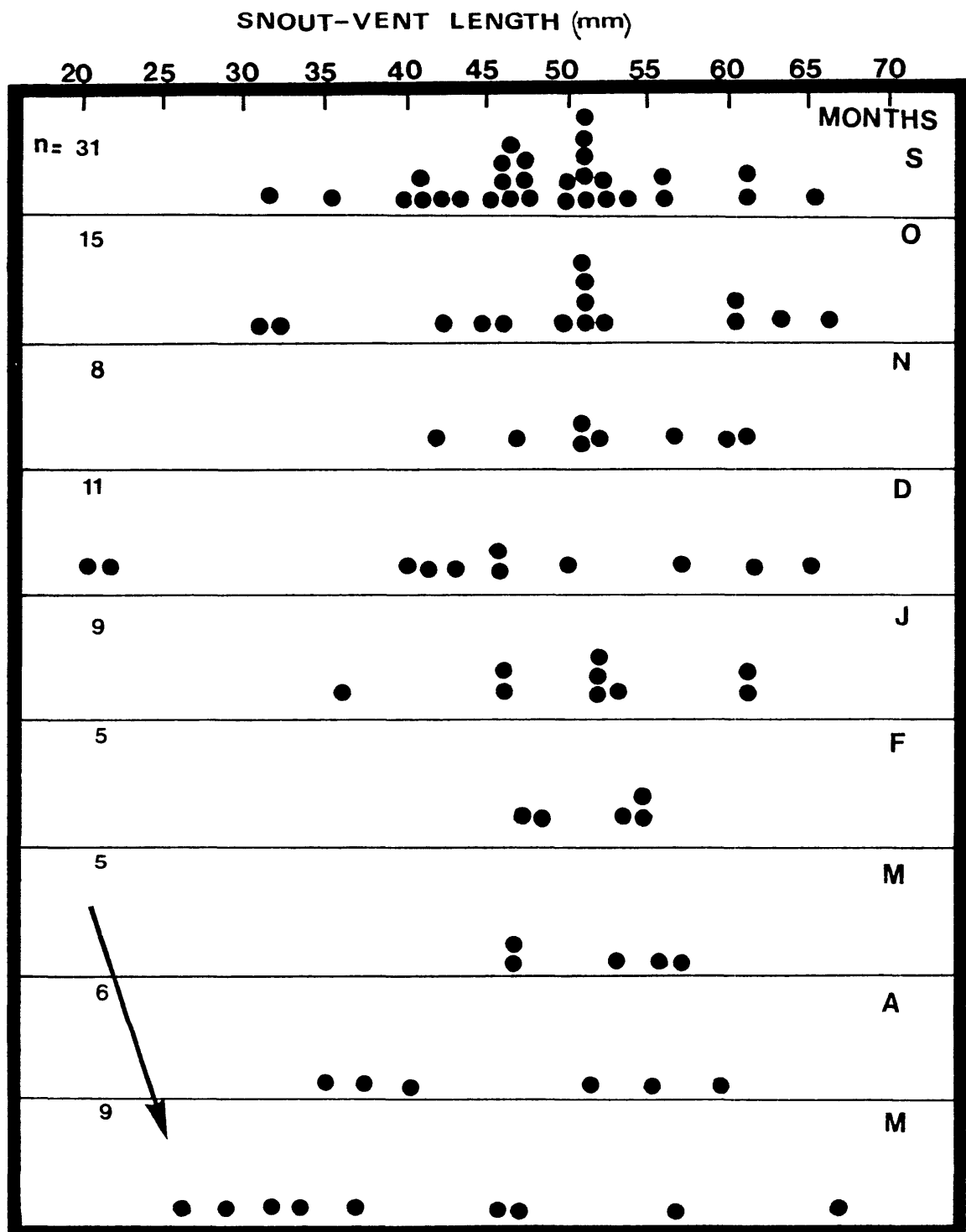
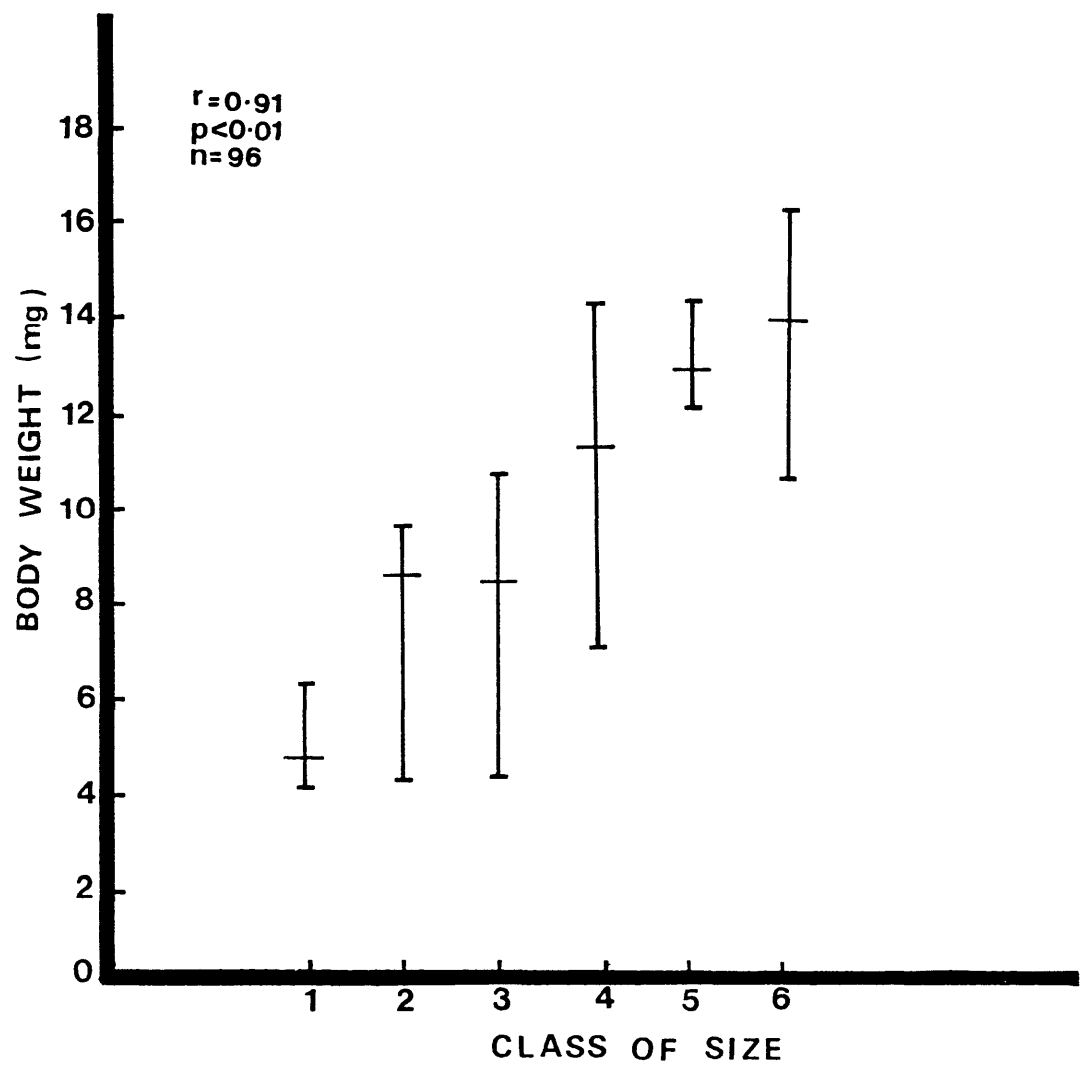of symbols.

SNOUT–VENT LENGTH (mm)

Figure 16. Relationship of snout-vent length and body

weight in 96 adult female *L. guichenoti*.

Horizontal lines represent sample means, and

vertical lines indicate ranges. Numbers

indicate sample sizes. Six size classes

(SVL) of 2.9 mm each were: (1) 27.0-29.9;

(2) 30.0-32.9; (3) 33.0-35.9; (4) 36.0-

38.9; (5) 39.0-41.9; (6) 42.0-44.9 mm SVL.

age/size the umbilical scar is healed (see also Fig. 15). They emerge
from brumation at a minimum body size of 31.0 mm SVL (Fig. 15).

In *L. guichenoti* females, weight increased significantly with body
length (r = 0.91, P < 0.01, df = 94) (Fig. 16). This increase was at
the rate of 0.5 g in first year reproductives (26.6-36.8 mm SVL) for
every 6 mm increase in body size (SVL) and 0.3 g for the same difference
in body length in second year reproductives (36.9-38.8 mm SVL). Among
reproductives over 2 years (38.9-46.0 mm SVL), for every 6 mm increase
in body length there was 0.3 g increase in body weight or only half that
observed in young animals. A similar statistically significant relation-
ship was found between body weight and body length of males (r = 0.89,
P < 0.01, df = 87).

Tail length increased with increase in body size in females (r =
0.32, P < 0.01, df = 94) (Fig. 17) and males (r = 0.35, P < 0.01, df =
96). The increase in tail length was at the rate of 10 mm among young
reproductive females for every 6 mm increase in body size (SVL).
Similarly, in second year reproductives, tail length increased at the
rate of 6 mm for every 6 mm increase in SVL. But reproductives of over
2 years of age differed in that tail length increased by 8 mm for every
6 mm increase in body size (SVL)(Fig. 17).

Body weight of adult *L. guichenoti* males increased with increase
in tail length (r = 0.35, P < 0.05, df = 54) (Fig. 18). Such was also
the case for females (r = 0.32, P < 0.05, df = 48). Based on 17 hatch-
lings with non-regenerated tails, tail length was slightly longer than
snout-vent length (100.2%) on the average. Similar calculations for 36
adult males showed tail length to average 100.4% of snout-vent length.
In 37 adult females the value was 100.3%. In this species, tail is nearly
the same as body length at birth, but this relationship shifts in adults
and tail length of both sexes is approximately 1½ times longer than snout-
vent length.

Figure 17. Snout-vent length and tail length in 96 female

adult *L. guichenoti*. See Fig. 16 for explanation

of symbols, and size classes.
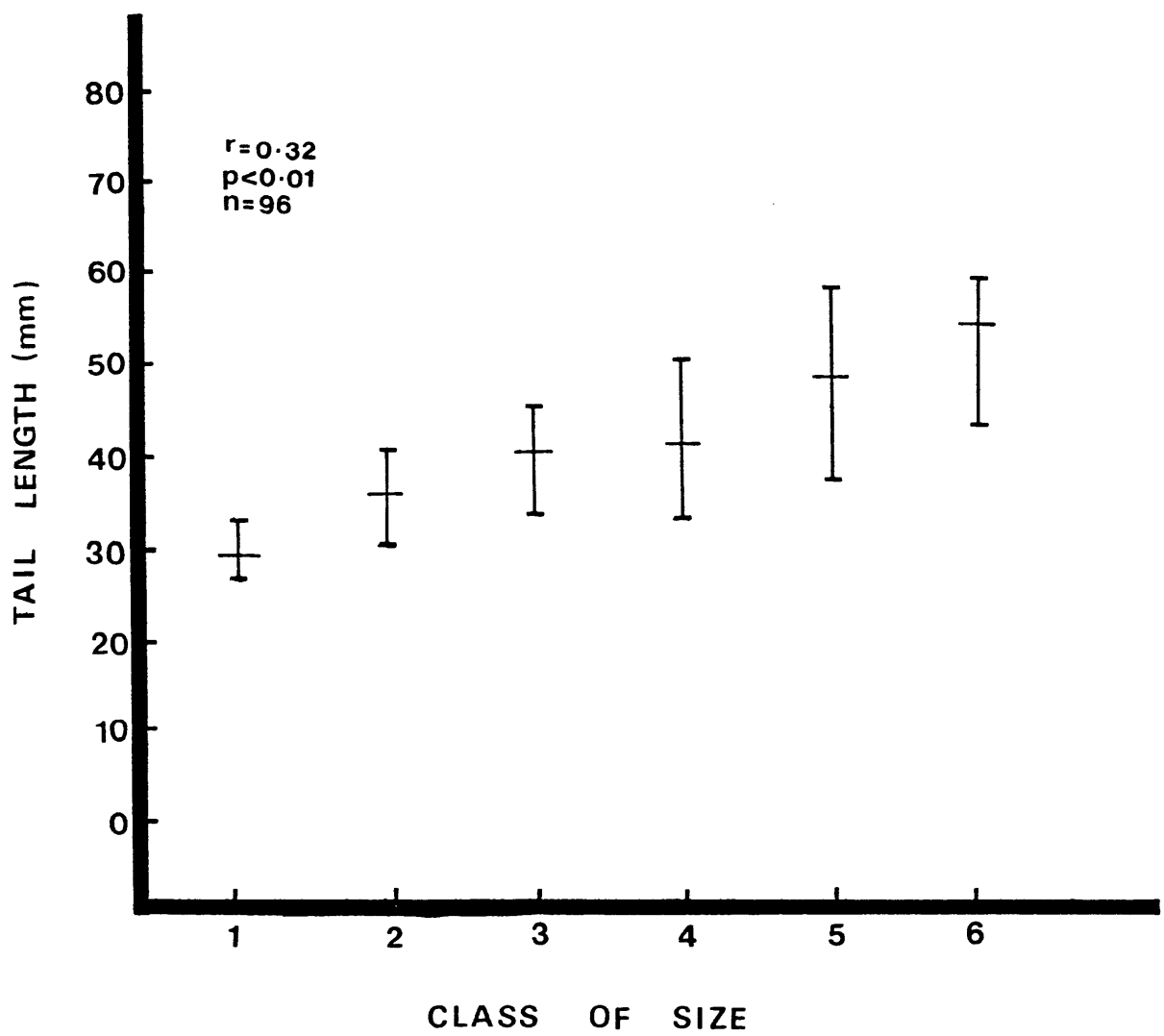
Figure 18. The relationship of body weight and tail

length in 54 adult male *L. guichenoti* .
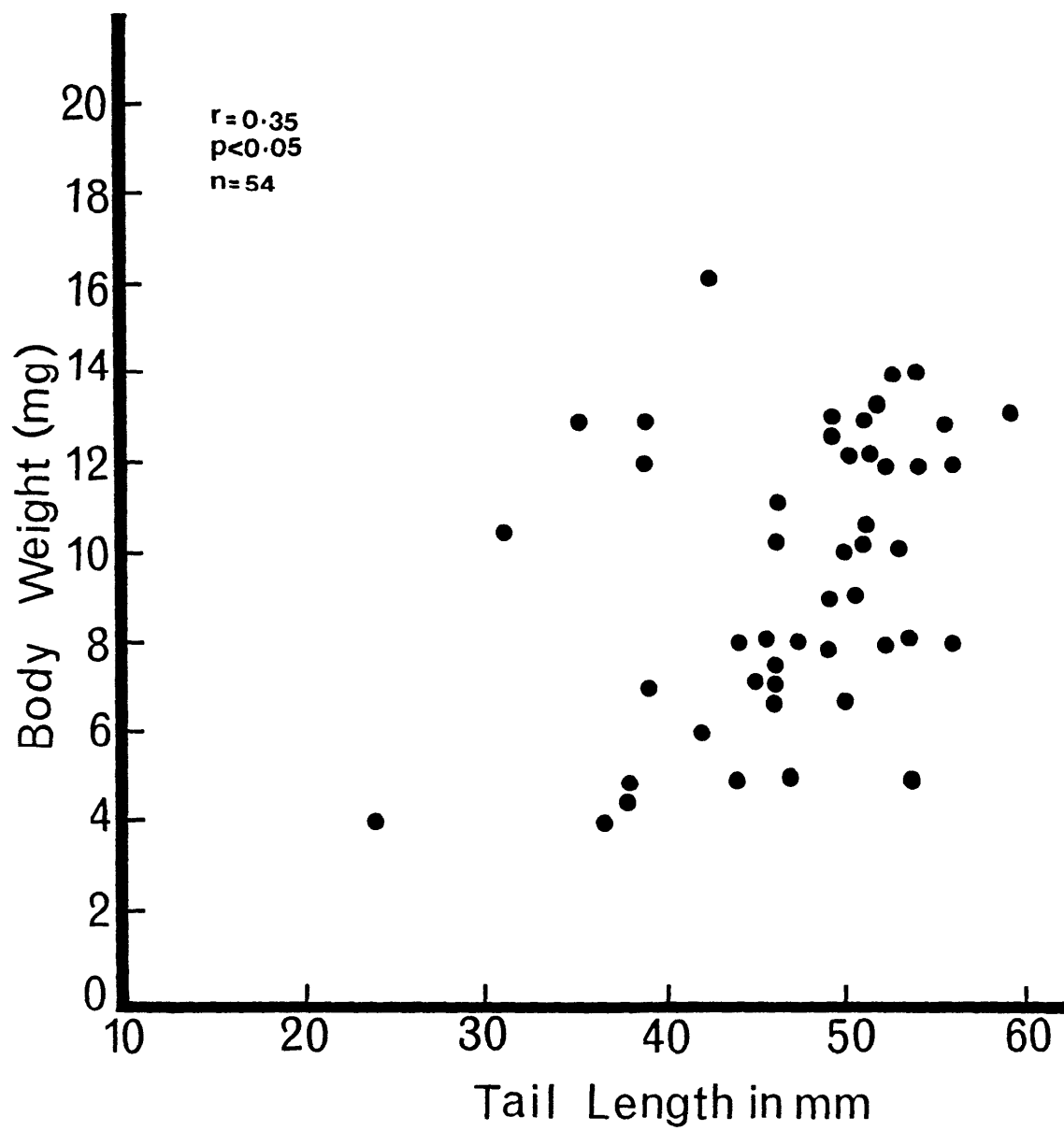
Figure 19. Relationship of snout-vent length and body weight

in 66 female and 44 male *H. decresiensis*.

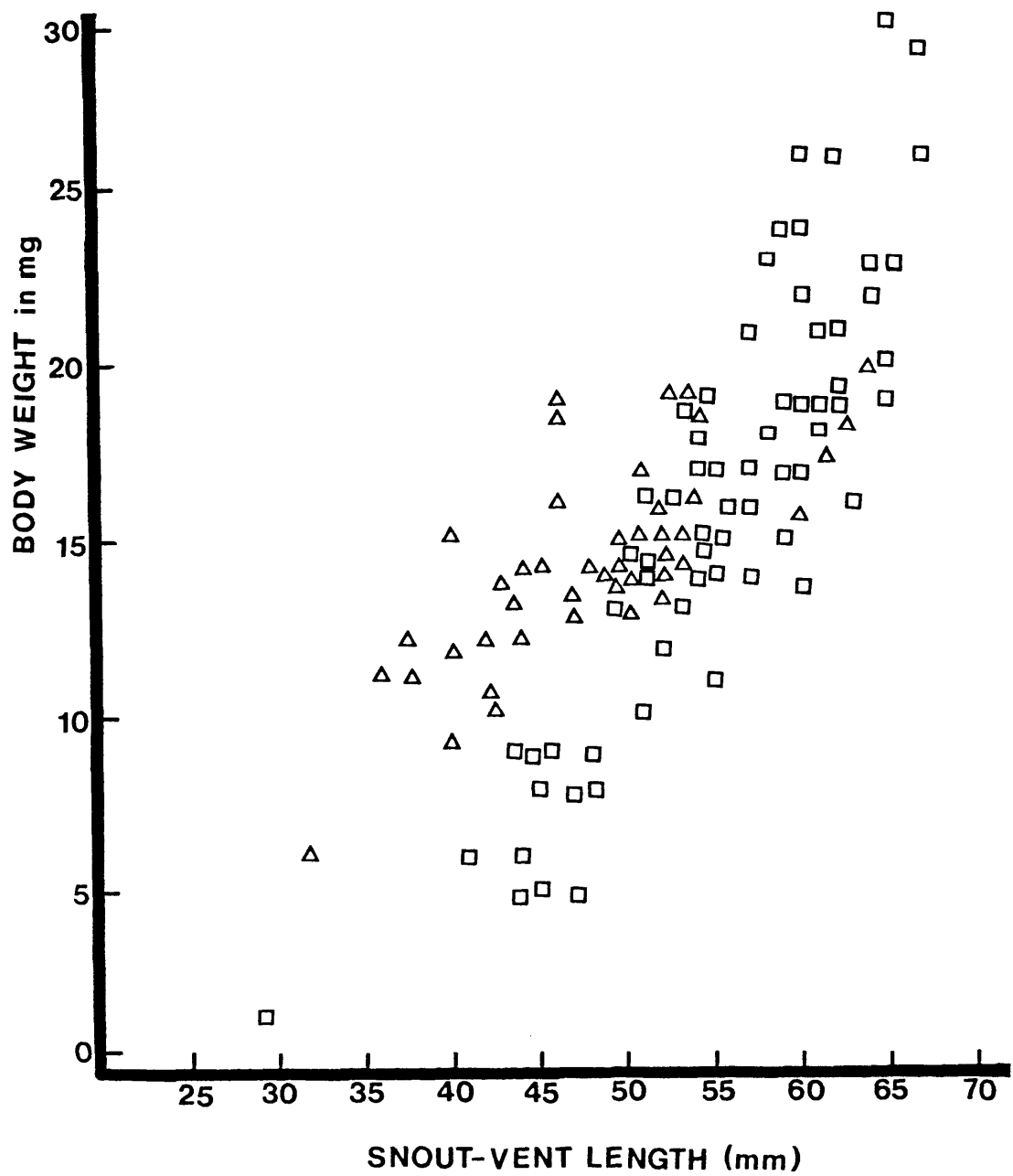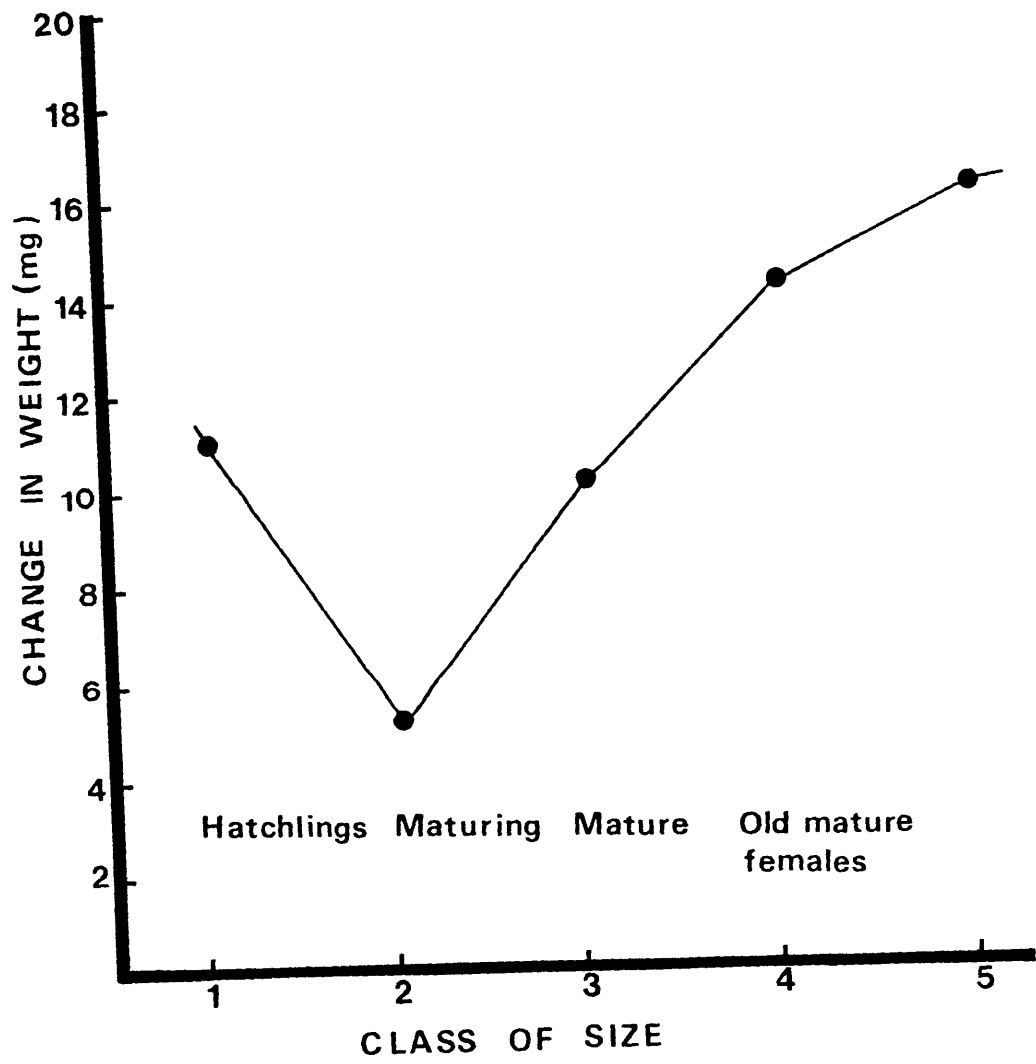SNOUT-VENT LENGTH (mm)

Figure 20.   Changes in body weight with increasing body length

(SVL).   Class of size, 1 = 30.0-36.9;   2 =

37.0-43.9;   3 = 44.0-50.9;   4 = 51.0-57.9;

5 = 58.0-64.9 mm SVL of 66 female

*H. decresiensis* (based on Fig. 19).

Tail length in adult male *H. decresiensis* increased steadily with increase in snout-vent length (r = 0.64, P < 0.01, df = 51). Female adults showed a similar relationship (r = 0.41, P < 0.01, df = 53). Unlike *L. guichenoti*, the relationship of tail to body weight was not significantly related in *H. decresiensis* males (r = 0.27, P > 0.05, df = 28) or females (r = 0.29, P > 0.05, df = 28).

Tail length of 10 newborn of *H. decresiensis* was longer on the average than snout-vent length (100.3%). A similar relationship in 26 adult males was 100.2% whilst that of 32 females was 100.1%.

The relationship of weight to body length (SVL) showed a highly significant statistical relationship in 66 adult *H. decresiensis* females (r = 0.90, P < 0.01, df = 64). A similar relationship was found among 44 adult males (r = 0.77, P < 0.01, df = 42) (Fig. 19). Subadults increased in weight rapidly and for every 6 mm increase in length (among 30-36 mm SVL) there was a 1.1 g increase in body weight. Similar change in body size in the 37 to 43 mm SVL female group corresponded with a 1.0 g increase in body weight. At sexual maturity, i.e. about 45 mm SVL, a similar size change of 6 mm corresponded with an increase on only 0.75 g body weight. A shift in growth pattern occurred after sexual maturity (Fig. 19). Every 6 mm increase in adult female (48.0-54.0 mm SVL) size, corresponded with 1.4 g increase in body weight. This relationship was the same in the 55.0 to 61.0 mm size group. However, in size groups greater than 61.0 mm SVL the relationship was found to be 1.9 g for every 6 mm increase in SVL. A similar discontinuous pattern of growth at specific levels of development, i.e. subadults, sexually mature and older individuals, was also found among males, and the relationship between increase in snout-vent length and body weight of both sexes were nearly identical (Fig. 19). Figure 20 shows the relationship between change in body weight and snout-vent length during different phases in the life cycle of *H. decresiensis*.

Figure 21. Size-specific growth patterns of juveniles

and female *L. guichenoti*. Lines connect

successive recaptures for individual lizards.

SNOUT-VENT LENGTH IN MM

15 20 25 30 35 40

S O N D J F M A

Spring   Summer   Autumn

MONTHS
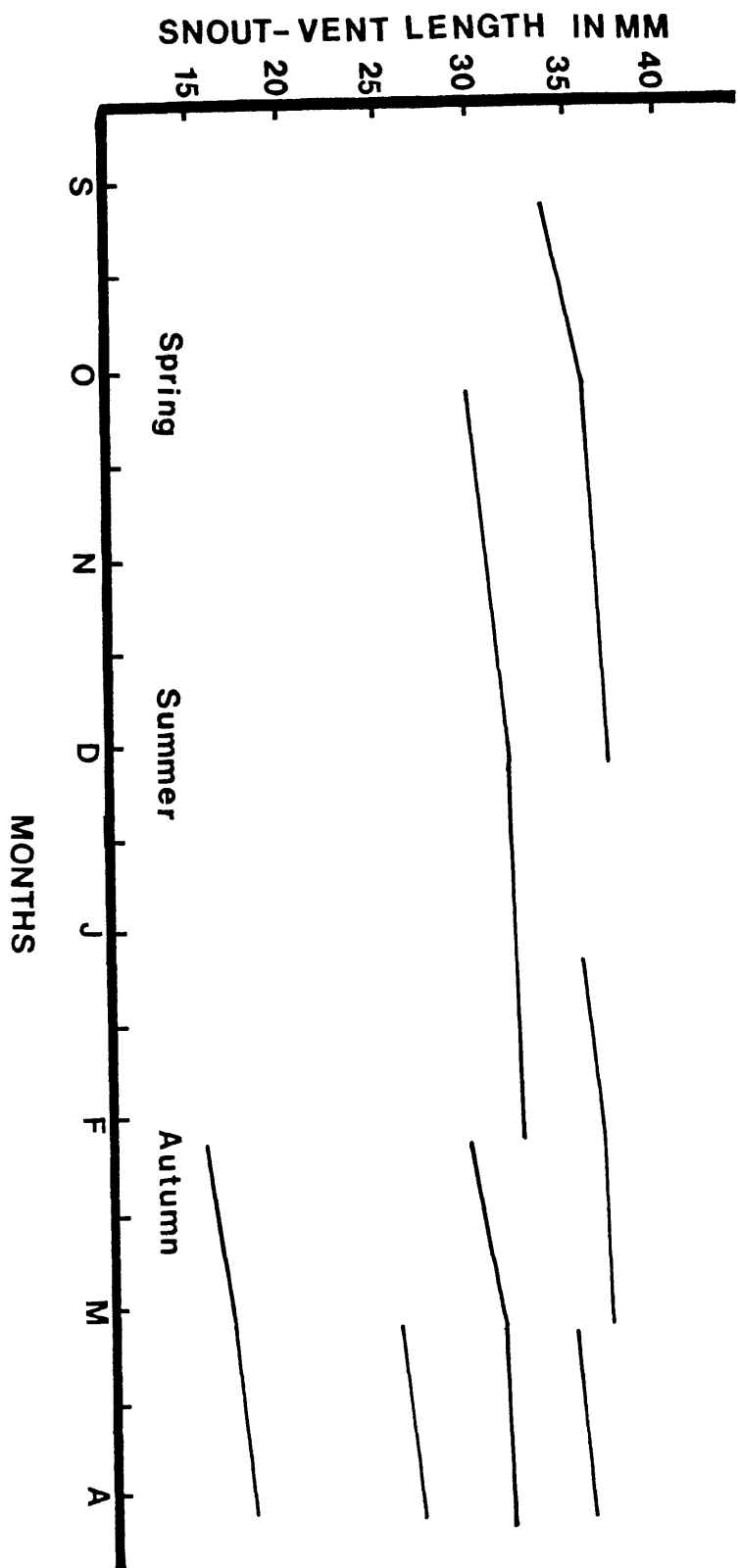
Eighty-six *L. guichenoti* (24 hatchlings: 62 adults) were

marked and released in the summers of 1982 and 1983 and of these,

8(9.3%) were recovered and 5(5.8%) of them recaptured twice after

the initial capture and marking   (Fig. 21). Figure 21 summarizes

the body size (SVL) increases in animals of various age/size classes

in different seasons over a period of 2 years. A hatchling marked

in summer showed a growth rate of 0.03 mm in SVL per day. Individuals

that had just reached sexual maturity (26-34 mm SVL) showed only a

slight increase of 0.04 mm in SVL per day. This growth rate declined

rather drastically in a group of 34.1-40.4 mm SVL to only 0.01 mm

growth per day. Maximum growth was in summer and

autumn. In spring, growth rate slowed down and tended to level out

towards an asymptote (Fig. 21). Survival of newborn lizards was low

and out of 24 marked hatchlings in February 1982 and 1983 respectively,

only 1(4.2%) was recovered, leaving 23 (95.8%) not recaptured.

DISCUSSION

In both sexes of *Lampropholis guichenoti* and *Hemiergis decre-*

siensis, body weight increased with increase in snout-vent length;

hence larger (and probably older) individuals weighed more than

smaller (younger) members of the same sexes and species (see also

Schoener and Schoener, 1978). However, these skinks were character-

ized by slow growth at some phases of the life cycle. Pengilley

(1972) also found a similar growth pattern among skinks he studied

and found growth rate in *Leiolopisma entrecasteauxi* individuals over

50.0 mm SVL to be extremely slow. Hatchlings or newborn tended to

put on weight at a greater rate than growth in body size (SVL).

This resulted in a curvilinear growth pattern in subadults. A similar

phenomenon occurs in *Lygodactylus chobiensis* subadults (Simbotwe, 1983a). A shift to a linear relationship occurs among sexually mature individuals. This also occurs in snakes (Kaufman and Gibbons, 1975) and some other lizards (Chapman and Chapman, 1964; Simbotwe, 1983a; but see also Andrews, 1982 for details). In both the present species tail length increased steadily with snout-vent length. The ratio of snout-vent length to tail length varied with size and age. In *L. guichenoti*, at hatching tail length is only slightly greater than snout-vent length, but the ratio becomes higher in adults of both sexes, and tail length in this species is nearly $1\frac{1}{2}$ times greater than snout-vent length in adulthood. Tail length increase in both sexes of *L. guichenoti* corresponded with nearly equal increase in body weight, i.e. individuals with longer tails tended also to weigh more.

In hatchlings of *H. decresiensis*, snout-vent length to tail length ratios were higher and tail lengths were greater than snout-vent length, but tail length in adults and especially among females was almost equal to that of snout-vent length. These differences may be a result of size/class or age, and sex specific differences in tail loss frequency and the nature of tail regeneration. In *Agama agama*, Chapman and Chapman (1964) found that tail length in young lizards, was about twice that of snout-vent length, similar to the present results but as in *Hemiergis decresiensis*, the older the animals were, the relatively shorter were their tails. Unlike *L. guichenoti*, tail length and body weight in *H. decresiensis*, showed a weak correlation that was not statistically significant. This could be because the tail in *H. decresiensis* acts as an energy (fat) storage organ (Robertson, 1981). There is also a possibility that tails of old specimens had been broken at some time and had regenerated in such a manner as to appear

undamaged. Reduction in body growth following tail loss in lizards

has been reported by Congdon *et al.*, 1974; Vitt *et al.*, 1977;

Ballinger and Tinkle, 1979. Poor nutrition and food storage, differ-

ences in tail loss frequency, incidence of mating and gravidity, and

differential tail regeneration frequency including population density

could retard growth in both body weight and length (Tinkle, 1967;

Smith, 1976; Ballinger and Congdon, 1980 and Dunham, 1981). Hatchlings

showed high rates of individual growth in body size. These declined

steadily among individuals that had just reached sexual maturity.

Growth was minimal in older specimens (Pengilley 1972) and eventually

reached an asympotote. Schoener and Schoener (1978) showed growth

rate differences among sexes and populations; in *Anolis sagrei* such

populations were only a few hundred metres apart. Variability in

growth rates among adult lizards and their juveniles, and survivorship

result in size frequency variation in a population and age at maturity.

Fitch (1973b) classified such populations into four types: (1) type 1

populations that show no temporal change in the level of reproduction

and stability, with individuals of all sizes and ages occurring in un-

varying ratios, (2) type 2 populations, similar to type 1 but with

individuals of all ages always present in constantly varying ratios,

(3) type 3 populations, which have an extended breeding season and a

non-breeding season of comparable duration; such a population is

characterized by a predominance of adults at the beginning of the

reproductive season and a variety of age/size groups at the end of the

breeding season, (4) type 4 populations which are structured with distinct

annual age groups (characteristic of most lizards in the temperate zone;

see Fitch, 1973b and Chapter 6 for details). Some workers have suggested

that differences in population size and age structure could come about

in a number of ways including (1) constant age at maturity accompanied

by variable growth of juveniles, (2) constant growth rates of juveniles and variable age at maturity or (3) a combination of these factors (see comments in Tollestrup, 1982). In species like *L. guichenoti* and *H. decresiensis*, in which young are produced following the winter inactivity period (similar to type 4 of Fitch, 1973b), time of birth or hatching is crucial since it determines the number of days remaining in which individuals may forage before the onset of winter. Cold winters at Newholme do not allow winter foraging. Hence, time of birth or hatching, time of egg deposition, size of eggs, and local variation in food resource levels may contribute greatly to variation in snout-vent length of juveniles. The years 1981 and 1982 were unusually dry (Chapter 1, part 2). The advent of good rains in the 1983 and 1984 seasons resulted in increase in body size (SVL) of both sexes of *L. guichenoti* and in mean body weights of females compared to the same population in previous years (Chapter 3; part 2), perhaps because of increased food availability. Even though food abundance was not measured, increase or decrease in food has been found to result in year to year variation in body growth rates in an iguanidae lizard, *Sceloporus scalaris* (Ballinger and Congdon, 1980). Unlike Porter (1972) who suggested that growth in reptiles continues throughout life, this study has shown that growth in adults declines drastically past sexual maturity and is minimal among older individuals. Pengilley (1972) arrived at the same conclusion, confirming the commonly accepted view that energy used for growth is shared among other energy demanding aspects of maintenance and reproduction.

Population size structure is dealt with in detail in Chapter 6 whereas tail loss and regeneration is discussed again at length in Chapter 3, part 2.

PART 2

CHAPTER 3

BODY SIZE, BODY SHAPE AND TAIL LOSS

INTRODUCTION

Organismal development results in characteristic body sizes
and body shapes that may vary phylogenetically and with sex (Stearns
1984). Body size, body shape and developmental timing are inter-
related phenomena, and a change in one may change the others (Bonner
and Horn, 1982). More detailed studies of the aforesaid factors,
how they are interrelated and how they affect each other were
published by de Beer (1958) and Gould (1977). Gould, provided a
static model which he used to illustrate the interactive aspects of
size, shape and timing (see also Alberch, Gould, Oster and Wake, 1979
for a less static model). Bonner and Horn (1982) discussed in detail
the aspects of the clock model relating to size, shape and timing and
also provided a list of questions that badly need answers. These
authors pointed out that change in size of an organism affect its
shape. The only attempt at studying body size and body shape in
lizards is that by Vitt and Congdon (1978). They found that body
shape of the lizards they studied was related to relative clutch mass
(RCM), and was therefore adaptive. Short or robust lizards, e.g.
Phrynosoma, were found to exhibit high reproductive output. Robust
lizards are often short whereas streamlined lizards are often longer
and less robust. Body size and body shape in lizards has been asso-
ciated with clutch volume and reproductive potential, predator escape,
foraging modes and microhabitat. Generally the body size and shape
of lizards complements their habits   (Vitt and Congdon, 1978; Vitt,

1981). Body shape offers an important design barrier to clutch volume in lizards. Simbotwe (1978) showed that in streamlined *Eumeces obsoletus* there is an inverse, relationship between size of eggs and number of eggs in a clutch. Stamps and Tollestrup (1984) have shown recently that change in body size of lizards may mean change in microhabitats or home sites. Juveniles of *Anolis aeneus* emigrate to habitats in shady areas when they become subadults. This ontogenic shift in habitat may relate to improved predator escape and improved ability to establish residency in an area (Stamps and Tollestrup, 1984).

There is no doubt now that most correlations of clutch size, age at maturity or mode of reproduction in reptiles seem to result from shared correlations with size (Stearns, 1984). Reduction in body growth following tail loss in lizards has been reported by Congdon *et al.* (1974), Vitt *et al.* (1977), and Ballinger and Tinkle (1979). In *Hemiergis decresiensis* the tail acts as an energy (fat) storage organ (Robertson, 1981). The tail in lizards is also known to function in running and balancing as a distraction to predators and among social lizards, in social encounters. There are few studies of lizard morphology linked to reproduction, longevity and survival, age at first reproduction, behaviour and microhabitat association and none on Australian skinks. Hence an aim of this study was to provide data on the aforementioned subjects and try to show how various factors interact.

MATERIAL AND METHODS

Lizards collected at monthly intervals were used for studies of
quantitative metric characters including tail loss. Snout-vent length
(SVL), body height (BH) and body width (BW) were measured by vernier
calipers to the nearest 0.1 mm. Head length (HL), head width (HW),
head height (HH) and tail length were measured in a similar manner.
Tails were classified as original, damaged or cut, or regenerated.
Body weight was recorded to the nearest 0.1 g using a pesola spring
balance.

Statistical analysis

A Mann-Whiney U-test and a student t test were used to relate
sex to body size (SVL) and to the various head measurements. Results
of non parametric and parametric tests were the same for all comparisons
but only results of parametric tests are reported here. A student t
test was used to relate body size (SVL), tail length (TL) and body
weight (BW) to sex-related differences. An interactive χ^2, employing
a G test was used to test the null hypothesis that there was no
difference in frequency in tail loss between sexes (Sokal and Rohlf,
1969; 592).

Analysis of covariance (ANCOVA) was used to show how body size
(SVL) varies with aforesaid head measurements in adult male and female
L. guichenoti.

RESULTS

Figure 22 presents body size (SVL) differences between male

L. guichenoti and *H. decresiensis* (maximum snout-vent lengths 43

mm and 64 mm respectively). Similarly, females had maximum snout-

vent lengths of 45 mm and 67 mm respectively (see also Tables 5

and 6). *Lampropholis guichenoti* is smaller than sympatric *Hemiergis*

decresiensis. Based on data from 1981 to 1982, female *L. guichenoti*

were larger than males, but this difference was not statistically

significant (t = 1.66, P > 0.099, N = 204; see also Table 7).

There is a statistically significant sexual difference between head

height (HH) (t = 2.37, P < 0.019, N = 177) and head width (HW) (t =

2.12, P < 0.036, N = 176). Data collected in the years 1983 and 1984

revealed a similar trend with female *L. guichenoti* being larger (SVL)

than their male conspecifics (t = 3.08, P < 0.01, df = 223) and

weighing more than males (t = 3.49, P < 0.001, df = 222). Body weight

of individuals from the dry years of 1981 and 1982 did not show sexual

differences (t = 1.8, P > 0.1, df = 187). In both years (1981-1982

and 1983-1984), females tended to have longer tails than males (maximum

tail lengths 69 mm and 67 mm; 62 mm and 61 mm respectively), but

this relationship was not significant in either case (t = 0.61,

P > 0.5, df = 95 and t = 1.51, P > 0.2, df = 88 respectively). Table

8 gives information concerning percentage frequency of tail loss and

tail regeneration in *L. guichenoti* males and females collected in the

1981 and 1982 season. There was a tendency for tail loss frequency to

increase among larger (hence older) individuals of both sexes (Table 8);

in males only adults (> 33.3 mm SVL) had broken and regenerated tails.

The null hypothesis that there was no difference in frequency of

broken and regenerated tails between male and female *L. guichenoti*

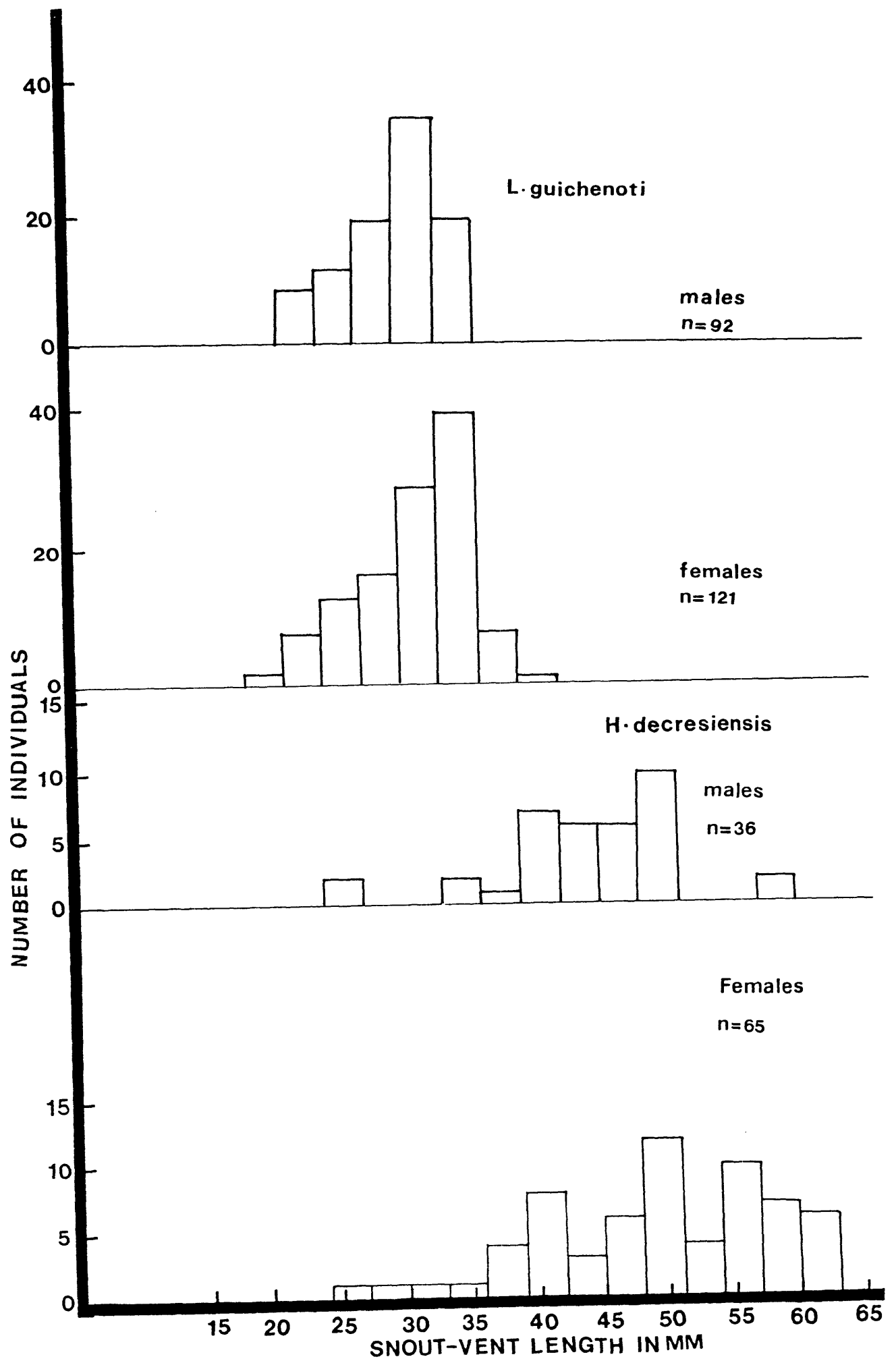Figure 22. Body size of lizards from Newholme, Armidale.

L·guichenoti

males
n=92

females
n=121

H·decresiensis

males
n=36

Females
n=65

NUMBER OF INDIVIDUALS

SNOUT-VENT LENGTH IN MM

Table 5. Morphological characteristics of *L. guichenoti*. Ranges are shown in parentheses and t-test values are males versus females.

Species	X̄ SVL ± SD (mm)	N	X̄ tail ± SD length	N	X̄ body ± SD weight	N
Lampropholis guichenoti						
1981-1982						
Males	35.95 ± 3.58 (27.0 - 43.0)	103	48.27 ± 7.62 (38.4 - 67.4)	55	0.97 ± 0.32 (0.4 - 1.5)	93
Females	36.86 ± 4.24 (26.0 - 45.0)	103	47.13 ± 10.94 (33.7 - 69.7)	42	1.06 ± 0.36 (0.3 - 1.6)	96
t	1.66		0.61		1.80	
P	>0.1		>0.9		>0.1	
df	204		95		187	
1983-1984						
Males	37.27 ± 3.21 (25.2 - 42.6)	89	52.96 ± 5.28 (31.0 - 61.5)	38	0.97 ± 0.26 (0.3 - 1.5)	89
Females	38.72 ± 3.60 (26.8 - 46.0)	136	50.72 ± 7.97 (36.6 - 62.0)	52	1.11 ± 0.32 (0.35 - 2.00)	135
t	3.08		1.51		3.49	
P	<0.01		>0.2		<0.001	
df	223		88		222	

Table 6. Sexual comparisons of snout-vent lengths and head
measurements of adult *H. decresiensis*. Ranges are
given in brackets.

Variable	x̄ ± SD	N	t-test value	Significant-level P
SVL				
Males	47.32 ± 6.37 (31.8 - 64.0)	49	9.06	< 0.001
Females	56.03 ± 3.83 (29.9 - 67.1)	65		
Head length				
Males	7.90 ± 0.77 (6.1 - 9.0)	25	2.71	< 0.01
Females	8.37 ± 0.73 (7.1 - 10.2)	65		
Head height				
Males	3.45 ± 0.37 (2.3 - 4.1)	30	1.35	> 0.2
Females	3.59 ± 0.48 (2.9 - 5.1)	46		
Head width				
Males	4.25 ± 0.43 (3.2 - 4.9)	30	3.28	< 0.01
Females	4.60 ± 0.47 (3.6 - 5.3)	46		
Tail length				
Males	56.40 ± 8.87 (42.6 - 65.0)	22	0.99	> 0.4
Females	59.05 ± 9.27) (30.5 - 68.9)	24		
Body weight				
Males	1.36 ± 0.34 (0.4 - 2.0)	49	2.75	< 0.01
Females	1.62 ± 0.59 (0.2 - 3.0)	65		

Table 7. Sexual comparison of snout-vent lengths and head
measurements of reproductive *Lampropholis guichenoti*
collected in the 1981-1982 season. Ranges are in
brackets.

	Mean (± SE)	N	t value	Degrees of freedom	Significant level 2-tailed p
SVL					
Males	35.95 ± 0.35 (27.0 - 43.0)	103	1.66	204	> 0.099
Females	36.86 ± 0.41 (26.0 - 45.0)	103			
Head length					
Males	8.60 ± 0.06 (6.8 - 10.0)	102	0.57	200	> 0.570
Females	8.55 ± 0.07 (6.8 - 10.1)	100			
Head height					
Males	4.90 ± 0.04 (2.4 - 5.4)	94	2.37	177	< 0.019
Females	4.72 ± 0.04 (2.4 - 5.1)	95			
Head width					
Males	3.74 ± 0.05 (2.5 - 6.0)	93	2.12	176	< 0.036
Females	3.60 ± 0.05 (2.5 - 5.8)	85			

Table 8. Percent frequency of lizards with broken and regenerated
tails separated by size and sex in *L. guichenoti* col-
lected in the 1981-1982 season. Sample sizes are given in
brackets.

SVL (mm)	Males		Females	
24 - 26.9	0	(10)	0	(10)
27 - 29.9	0	(12)	20.0	(5)
30 - 32.9	0	(5)	20.0	(5)
33 - 35.9	33.0	(9)	28.5	(7)
36 - 38.9	37.5	(16)	35.7	(14)
39 - 41.9	64.7	(17)	53.1	(17)
42 - 44.9	50.0	(2)	58.3	(12)
45 - 47.9	66.6	(3)	80.0	(5)

could not be rejected (χ^2 test, G = 6.86, P > 0.05, df = 4).

Table 9 provides a year to year comparison of morphological characteristics of *L. guichenoti*. The years 1981 and 1982 were unusually dry in comparison to the wet years of 1983 and 1984 (Chapter 1, part 2). There was a shift towards increased growth in body size (SVL) during the wet years among males (mean snout-vent lengths 35 mm and 37 mm respectively) (t = 2.69, P < 0.01, df = 190). A similar result was found among females (mean snout-vent lengths 36 mm and 38 mm) (t = 3.68, P < 0.001, df = 237) (see also Table 9).

Males from wet years compared with those from dry years showed a statistically significant difference in tail length (t = 3.28, P < .01, df = 91), but the opposite was true of females (t = 1.84, P > 0.1, df = 92). Males from wet and dry years did not show a statistically significant difference in mean body weight. The same was true of females (t = 1.15, P > 0.4, df = 229).

Table 10 provides information on the relationships of snout-vent length with tail and head measurements (head length (HL), head width (HW), head height (HH), body width (BW) and body height (BH). The ratios of body size (SVL) in relationship to the aforesaid parameters provides a measure of body form, i.e. size and shape. Smaller ratios reveal how streamlined in body form these two species are. *H. decresiensis* is more streamlined than *L. guichenoti* (Table 10). Except for tail length (TL), head width and body height ratios, the rest of the ratios showed statistically significant sexual differences (Table 10).

Table 11 shows how interrelated body size (SVL) is to the aforesaid head measurements in *L. guichenoti*. In males, this relationship is (ANCOVA): F (3,89) = 184.4, P < 0.001. A similar relationship in females is: F (3,88) = 213.20, P < 0.001 (see Table 11 for details).

Table 9. A yearly comparison of morphological characteristics of male and female *L. guichenoti*. Ranges are given in brackets and t-test values are males versus males and females versus females.

| Sex and Year	X̄ SVL ± SD	N	X̄ tail length ± SD	N	X̄ body weight ± SD	N
Males 1981–1982	35.95 ± 3.58 (27.0 – 43.0)	103	48.27 ± 7.62 (38.4 – 67.4)	55	0.97 ± 0.32 (0.4 – 1.5)	93
Males 1983–1984	37.27 ± 3.21 (25.2 – 42.6)	89	52.96 ± 5.28 (31.0 – 61.5)	38	0.97 ± 0.26 (0.3 – 1.5)	89
t	2.69		3.28		ns	
P	< 0.01		< 0.01			
df	190		91			
Females 1981–1982	36.86 ± 4.24 (26.0 – 45.0)	103	47.13 ± 10.9 (33.7 – 69.7)	42	1.06 ± 0.36 (0.3 – 1.6)	96
Females 1982–1984	38.72 ± 3.60 (26.8 – 46.0)	136	50.72 ± 7.9 (36.6 – 62.0)	52	1.11 ± 0.32 (0.35 – 2.0)	135
t	3.68		1.84		1.15	
P	< 0.001		> 0.1		> 0.4	
df	237		92		229	

Table 10. Morphological characteristics of *L. guichenoti* and *H. decresiensis*. Sample sizes are in brackets (t-tests are males versus females).

Species	Tail length/SVL X̄ ± SD	Head length/SVL X̄ ± SD	Head width/SVL X̄ ± SD	Head height/SVL X̄ ± SD	Body width/SVL X̄ ± SD	Body height/SVL X̄ ± SD
L. guichenoti Males	1.361 ± 0.15 (36)	0.238 ± 0.01 (70)	0.132 ± 0.03 (67)	0.104 ± 0.01 (67)	0.164 ± 0.03 (66)	0.138 ± 0.01 (64)
Females	1.308 ± 0.18 (37)	0.233 ± 0.01 (74)	0.127 ± 0.01 (74)	0.084 ± 0.03 (76)	0.185 ± 0.02 (76)	0.140 ± 0.02 (76)
t	1.36	2.98	1.36	5.19	4.95	0.72
P	> 0.2	< 0.01	> 0.2	< 0.001	< 0.001	> 0.5
df	71	142	139	137	140	138
H. decresiensis Males	1.257 ± 0.16 (26)	0.169 ± 0.01 (18)	0.078 ± 0.01 (31)	0.069 ± 0.01 (31)	0.118 ± 0.01 (29)	0.091 ± 0.01 (28)
Females	0.989 ± 0.14 (32)	0.152 ± 0.01 (64)	0.084 ± 0.01 (46)	0.065 ± 0.01 (46)	0.110 ± 0.01 (44)	0.88 ± 0.01 (44)
t	6.79	3.73	2.58	1.72	3.33	1.24
P	< 0.001	< 0.001	< 0.02	> 0.1	< 0.01	> 0.4
df	56	80	75	75	71	70

Table 11.   Analysis of covariance (ANCOVA) with SVL as the covariate for head measurements between the sexes of *L. guichenoti*. Sample size is given in brackets.

Variable	Sum of squares	Mean squares	F value	F test (significant level)
Males				
Head height	1014.12844	338.04281	F =	184.14314, P < 0.001
Head length	163.38274	1.83576	(3,89)	
Head width				
Females				
Head height	1553.41224	571.80408	F	
Head length	213.71852	2.42862	(3,88) =	213.20922, P < 0.001
Head width				

Figure 23. Composition, sexual dimorphism and relative

tail breaks in samples of *H. decresiensis*.

Open circles and histograms represent males

while closed ones represent females (N=112).
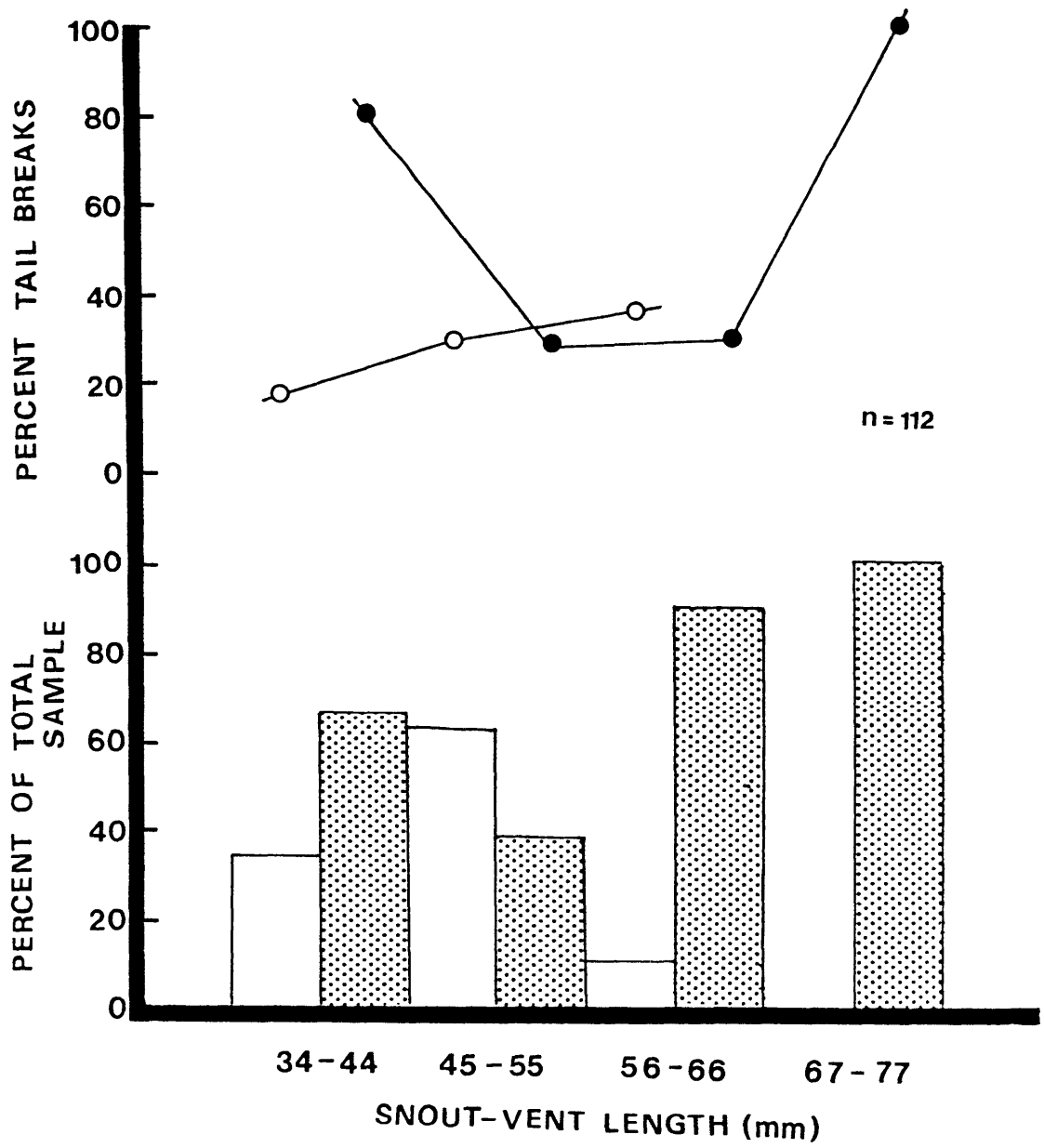
Female *Hemiergis decresiensis* are larger than males (maximum snout-vent lengths 67 mm and 64 mm respectively) (t = 9.06, P < 0.001, df = 112). Head length (t = 2.71, P < 0.01, df = 88), head width (t = 3.28, P < 0.01, df = 74), and body weight (t = 2.75, P < 0.01, df = 112) showed statistically significant sexual differences (Table 6). Females had longer tails than males (maximum tail lengths 59 mm and 56 mm respectively), but this difference was not statistically significant (t = 0.99, P > 0.4, df = 44). Table 10 provides information on the relationship of tail length, head width, head height, body width and body height to snout-vent length of adult *H. decresiensis*. The small ratios indicate how streamlined in body form this lizard is. Despite the larger body size (SVL) of *H. decresiensis*, it's head length is relatively smaller than that of *L. guichenoti*, but with a broader head width (see Tables 6 and 7 for a comparison). This relationship holds when intersexual comparisons are made between species. Based on ratios in Table 10, both male and female *H. decresiensis* have body shape that is narrower and more streamlined than that of either sex of *L. guichenoti*.

Figure 23 shows that in both sexes there are higher tail break frequencies in larger (older) *H. decresiensis* individuals.

A year to year comparison was not possible in *H. decresiensis* because of small sample sizes in the 1983–1984 study period.

DISCUSSION

Herpetologists studying lizards have for a long time recognized the relationship between body size at maturity, reproductive output (clutch size), survival and longevity. Vitt and Congdon (1978) related body shape of lizards to relative clutch mass (RCM). Even though developmental and genetic barriers are commonly known (Tinkle

et al., 1970 and Tinkle and Gibbons, 1977) no studies on lizards

have addressed specifically the ways in which size, shape and

developmental time are interrelated using the clock model of Gould

(1977) and Alberch *et al.* (1979). Recently Stearns (1984) showed

that in reptiles there are size effects and lineage-based constraints

on major aspects of life history phenomena. The present study showed

that both *H. decresiensis* and *L. guichenoti* have a streamlined body

form, well suited to life among piles of wood, rock crevices, grass

and litter. Vitt and Congdon (1978) showed that body shape and size

may co-evolve with clutch volume and that shape complements habits of

lizards. However, among the lizards they studied, they recognized

two forms (1) slow moving, robust, sit-and-wait foragers, and (2) fast-

moving, streamlined, wary, and actively searching foragers. Both

L. guichenoti and *H. decresiensis* fit the second category except that

the latter has weak limbs and hence moves more slowly. Moreover,

H. decresiensis shows peculiar morphology in that even though nearly

twice as large as *L. guichenoti,* it has a small, short head which is

wider and relatively flat. Such morphology in *Platynotus* is said to

be adaptive in that it allows individuals to seek refuge in narrow

crevices (Vitt, 1981). I also observed this behaviour in a rock-

dwelling population of Mexican lizards in 1977 during a collecting trip

to Nuevo Léon, Mexico.

Head size is important in considering the size of prey taken by

the respective species. Both *L. guichenoti* and *H. decresiensis* share

a 74.9% similarity in types of prey eaten (Chapter 2, part 1). In

the latter species prey size was found to be correlated with head length,

which suggests that as this lizard grows larger, it tends to take larger

prey items. Also, the spectrum of prey sizes likely to be eaten by large

lizards is greater than those available to smaller lizards which cannot

handle very large prey. Similarity in diet may reflect similar habits, microhabitat or behaviour. In Chapter 2, part 2, a 49.2% similarity in microhabitat was recorded between *L. guichenoti* and *H. decresiensis*. Both *L. guichenoti* and *H. decresiensis* resemble African lygosomine lizards *Lygosoma sundevallii*, *Panaspis walhebergii*, *Mabuya varia* in morphology and certain aspects of their ecology (see Simbotwe, 1984).

Even though the present study has not related energetics to body size, Karasov and Anderson (1984) recently said that energy assimilation and energy metabolism may set limits to production, i.e. to maintenance, growth and reproduction. Dry conditions may be correlated with low productivity and wetter years with high productivity (Chondropoulus *et al.* 1983). This could have been one reason for marked increase in body growth and improved reproductive performance in *L. guichenoti* during the wetter years (see also Chapter 4). Vitt *et al.* (1978), Dunham (1978), Ballinger and Congdon (1980) and Stamps and Tanaka (1981) discuss the consequences of temporal (year to year), spatial differences in prey availability on growth rate, body size and reproductive output in populations of lizards.

Tail breaks increased among larger (hence older) animals. A similar result was reported in the genus *Pordacis* by Chondropoulus and Lykakis (1983). Tail breaks and regeneration did not differ between the two sexes in *L. guichenoti*. Tinkle and Ballinger (1972) and Vitt *et al.* (1977) state that tail breaks may reveal differences in longevity between sexes (when intraspecific comparisons are made) or community structure (when populations are compared). Neither intra- specific fights between individuals nor home site defences were observed. Thus, discounting tail loss due to contests, the only plausible sources of tail breaks is by autotomy, resulting from attempted predation or from mechanical damage (like tail being caught

between objects). In *H. decresiensis* the tail is used as an energy (fat) storage organ. Hence one would intuitively expect reduced willingness to autotomize in this species. None of the individuals autotomized their tails in captivity whilst *L. guichenoti* commonly did so.