

CHAPTER 4

FEMALE REPRODUCTIVE CYCLE

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INTRODUCTION

Lindemann (1942) was one of the earliest workers who suggested that energy flow is the major force driving ecosystem function. Subsequently predictions of the outcome or direction of population or community evolution based on optimality principles have been made. Also, formulation of a set of problems which an organism is required to face and prediction of which kind of behaviour, morphology, and physiology constitute the best "solutions" to the problem are central to modern life history studies and research (Lewontin, 1979). Important aspects are (1) feeding rates and cost of obtaining food, (2) ability to extract energy from different kinds of foods, (3) predator escape, and (4) energy allocation into respiration, growth and reproduction.

Some of these topics have already been examined. Maintenance and growth were covered in detail in Chapters 2 and 3 respectively. Chapter 1, part 1 reviewed many of the female reproductive data published to date on skinks from all parts of the world including both tropical and temperate areas. Part 2 of Chapter 1 dealt with the environment.

Some workers have shown how important environmental variance is in determining life histories (Murphy, 1968; Wilbur *et al.*, 1974). Environmental variance has also been used to explain the evolution of "bet-hedging" life histories (Stearns, 1976). Schwaner (1980) discussed reproductive biology of skinks in American Samoa in relation to predictability and contingency in cyclic weather factors (rainfall

and temperature). Other studies have shown the importance of habitat to female reproduction (Vitt and Congdon, 1978; Vitt, 1981) the role of lipid stores (Hahn and Tinkle, 1965 ; Smyth, 1974), and the relation of food availability to female reproduction (Ballinger, 1977; Ballinger, 1983 and literature cited therein). Others have attempted to study in a general way the significance of diverse natural history schedules and have suggested optimal allocation of energy to reproduction, maintenance and growth (Cody, 1966; Williams, 1966; Gadgil and Bossert, 1970; Fagen, 1972; Pianka, 1976b).

Generally, breeding cycles of females may vary in any of the following characteristics: (1) age at maturity, (2) clutch size, (3) clutch frequency, (4) size of adult animal, (5) relative size of new born young or hatchlings. At the population level, there are forms that mature early (within a year) and produce one brood per year. Tinkle (1969) and Tinkle, Wilbur and Tilley (1970) indicated that these generally occur in the tropics where suitable breeding conditions occur all the year round. Late maturation (taking more than one year to mature), one brood per year, cyclic reproduction and few young produced per year, they designated as typical of seasonal temperate environments, in which only part of the year is climatically suitable for breeding. These ideas led to the concept of reproductive effort which originated in the work of Fisher (1930) and to the distinction between r- and K-selection (MacArthur and Wilson, 1967; Pianka, 1970, 1972; Gadgil and Solbrig, 1972). Many present day studies on reproductive biology of female lizards are based on these concepts.

Fitch (1970, 1982) summarized reproductive cycles in reptiles. The bulk of information on reproduction in Australian lizards occurs in the works of Barwick (1965), Hickman (1960), Pengilley (1972), Rawlinson (1974a, 1974b, 1975), Smyth and Smith (1968), Veron (1969) and Weekes

(1935). Reproductive condition in Australian skinks is summarized in Chapter 1, part 1 and the need for more detailed work is emphasized. The aim of the present chapter is to elucidate the female reproductive biology of two sympatric populations of lizards, *Lampropholis guichenoti* and *Hemierngis decresiences* inhabiting the New England tablelands.

MATERIAL AND METHODS

During autopsy, oviductal and ovarian egg length and width were recorded. Reproductive state was characterized using various stages of ovarian development as determined by ovarian follicular colour. They were: stage 1, the occurrence of a translucent cytoplasmic liquid in the ova, stage 2, a creamy coloured cytoplasm (primary growth) and stage 3, a yellowing due to yolk deposition (vitellogenesis). Numbers of translucent, creamy, ovarian follicles and oviductal eggs were recorded monthly for females. Sizes of oviductal eggs were measured to the nearest 0.05 mm using an eye piece micrometer.

Reproductive condition of lizards was judged as:

- (1) immature, for hatchlings and males with small underdeveloped testes (< 3.0 mm in size) lacking heavily convoluted semeniferous tubules and females with ova translucent or creamy (< 4.0 mm in size) and narrow oviducts,
- (2) mature, for males with slightly enlarged testes (> 3.0 mm in size) and poorly developed convoluted semeniferous tubules and females with yellowing ova (vitellogenesis) without distended oviducts,
- (3) old mature, for males with enlarged testes with heavily convoluted semeniferous tubules and females with oviductal eggs (ovigerous), and
- (4) older mature, for males in a condition similar to those of (3), but with greatly enlarged vascular testes and females with greatly enlarged oviducts and small developing ova (recently spent).

While arbitrary, this classification helps in characterizing the reproductive condition of males and females into age/size classes of recognizable reproductive condition (Schwaner, 1980).

Sex ratios from samples collected monthly were computed, together with the relative position of the left to the right ovary. Soft morphology was described. Abdominal fat bodies were weighed to the nearest 0.1 g.

Statistical Analysis

Spearman Rank Correlation Coefficients (r_s) were used to determine rank correlation of clutch size to body size (SVL of females) and the product moment correlation coefficients (r), was used to test whether testicular recrudescence or ovarian growth is correlated with rainfall and ambient temperature. A student t-test was used to test mean clutch differences between years in *L. guichenoti* and a paired t-test was used to test differences in egg number between right and left oviducts. An interactive chi-square employing a G test was used to test departures in secondary sex ratios.

Small sample sizes of *H. decresiensis* precluded detailed analysis of reproductive biology.

RESULTS

Timing of reproduction in L. guichenoti

Brumation commences in late May and lasts up to September at Newholme. Length of the brumation period depends on the prevailing weather during a given year.

The reproductive period begins with formation of ova in the ovaries in spring followed by ovulation and egg deposition in late November to early December (Fig. 24). Hatching of eggs occurs in February to early

Figure 24. Seasonal variation in mean testis size (mm) and percentage of gravid females. Seasonal rainfall and mean monthly maximum temperature appears in the upper figure. Sample sizes for females with oviductal eggs are shown on Figures 25 and 34. Squares and open bars represent 1981 and triangles and closed bars represent 1982.

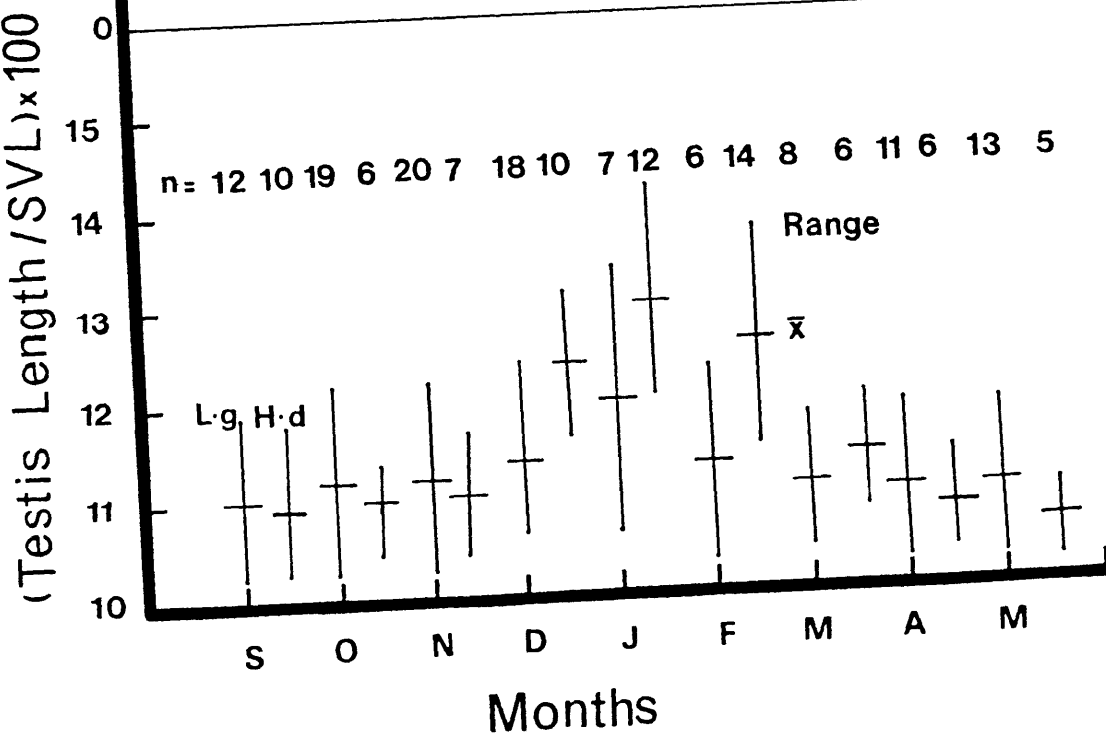
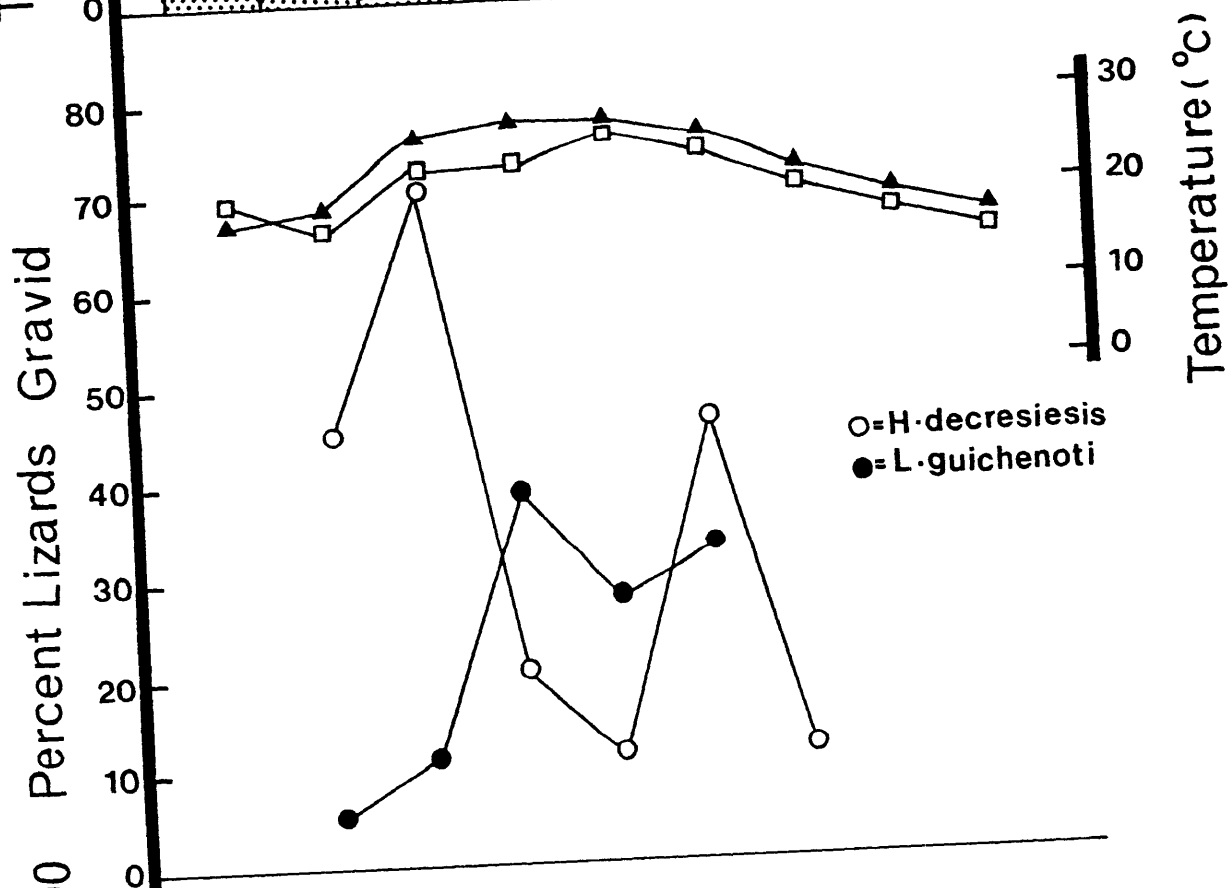
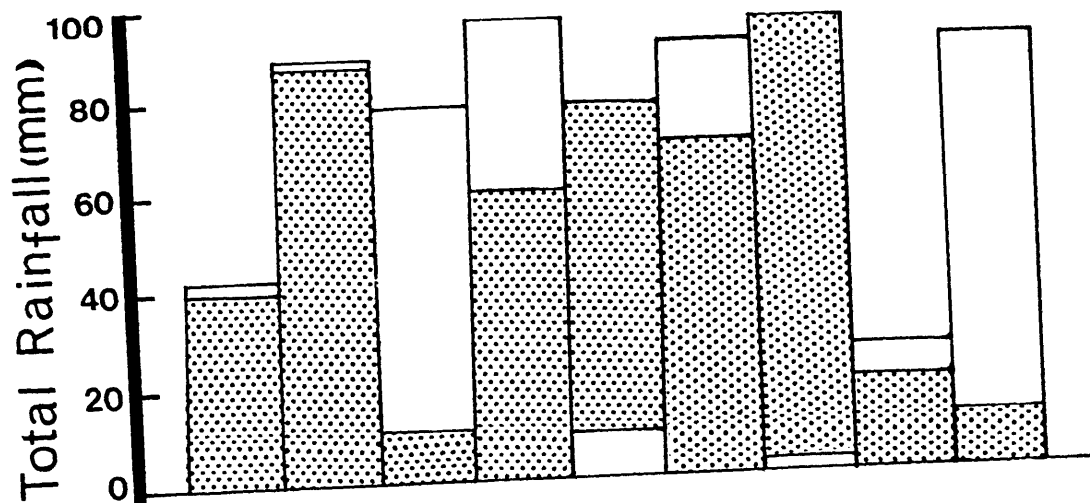


Figure 25. Reproductive state of female *L. guichenoti* during the 1981-1982 season. Numbers of females appear on each bar.

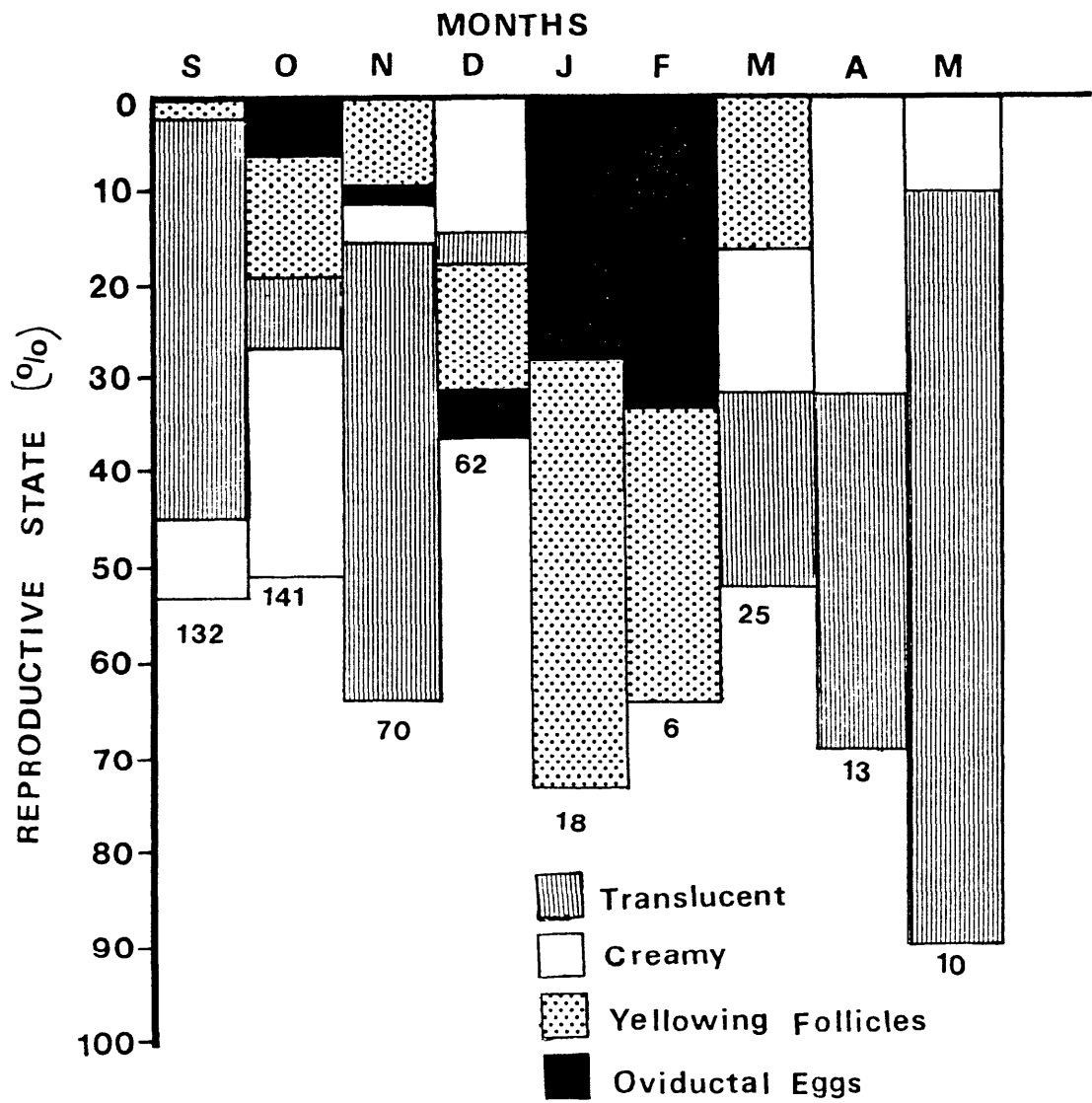


TABLE 12. Monthly distribution of ovarian follicles and oviductal eggs in sexually mature female *Lampropholis guichenoti* (SVL > 34.0 mm). Percentages in parentheses.

Months and years 1981-82	Sample size	Ovarian follicles (mm)			oviductal eggs
		translucent	creamy	yellowing	
		< 1.9	2.0-3.9	4.0-5.8	5.9-10.2 mm size
September	132	60 (45.5)	70 (53.0)	2 (1.5)	0
October	141	37 (26.2)	71 (50.0)	27 (19.1)	6 (4.3)
November	70	45 (64.3)	11 (15.7)	6 (8.6)	8 (11.4)
December	62	11 (17.70)	8 (12.9)	19 (30.7)	24 (38.7)
January	18	-	-	13 (72.3)	5 (27.7)
February	6	-	-	4 (66.6)	2 (33.4)
March	25	13 (52.0)	8 (32.0)	4 (16.0)	-
April	13	9 (69.2)	4 (30.8)	-	-
May	10	9 (90.0)	1 (10.0)	-	-

Figure 26. Seasonal changes in mean length (mm) of yellowing follicles and length of oviductal eggs in adult female *L. guichenoti*.

Range, mean, standard deviations of the mean are given and sample sizes are shown on the graph.

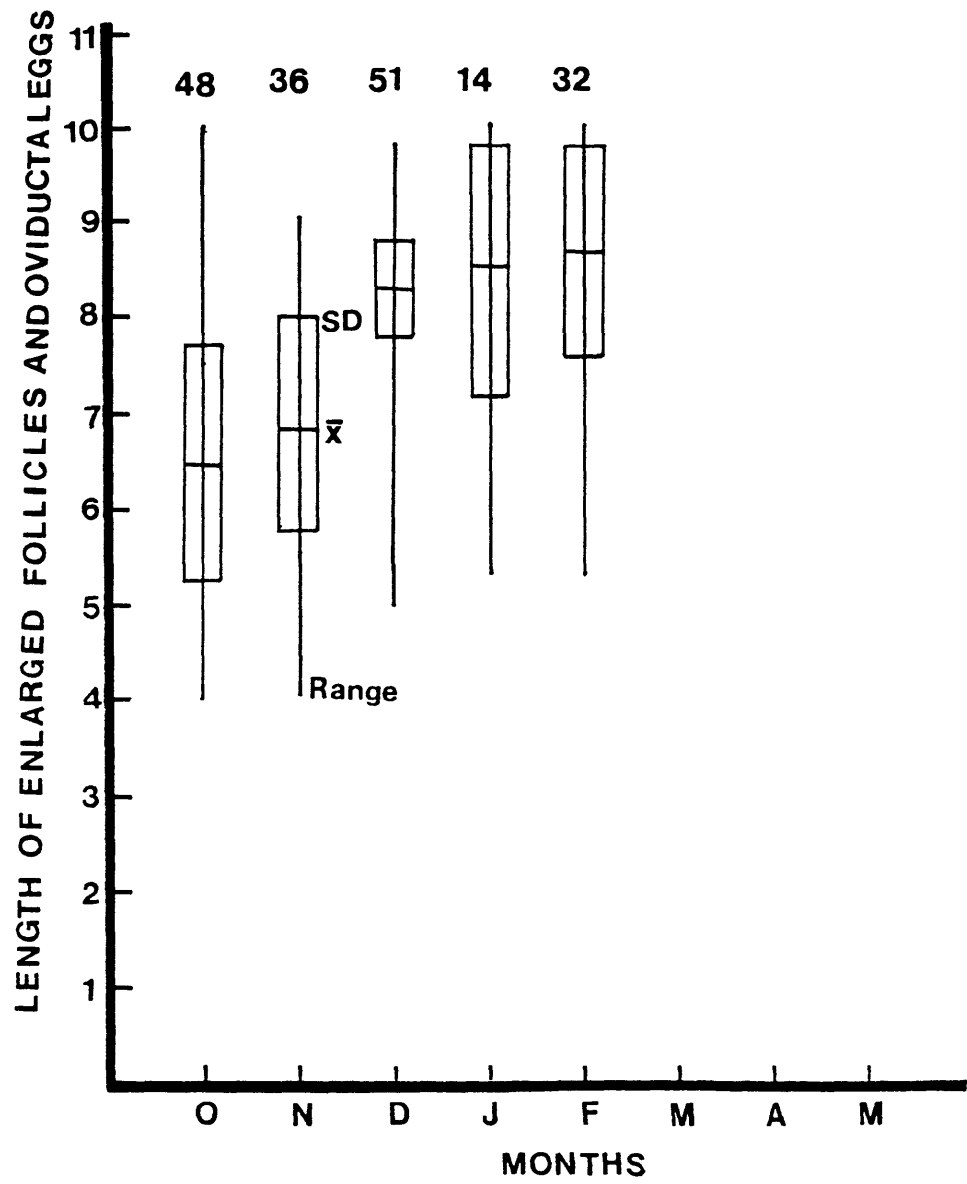


Figure 27. Reproductive state of female *L. guichenoti* during the 1983-1984 season. Sample sizes appear on each bar.

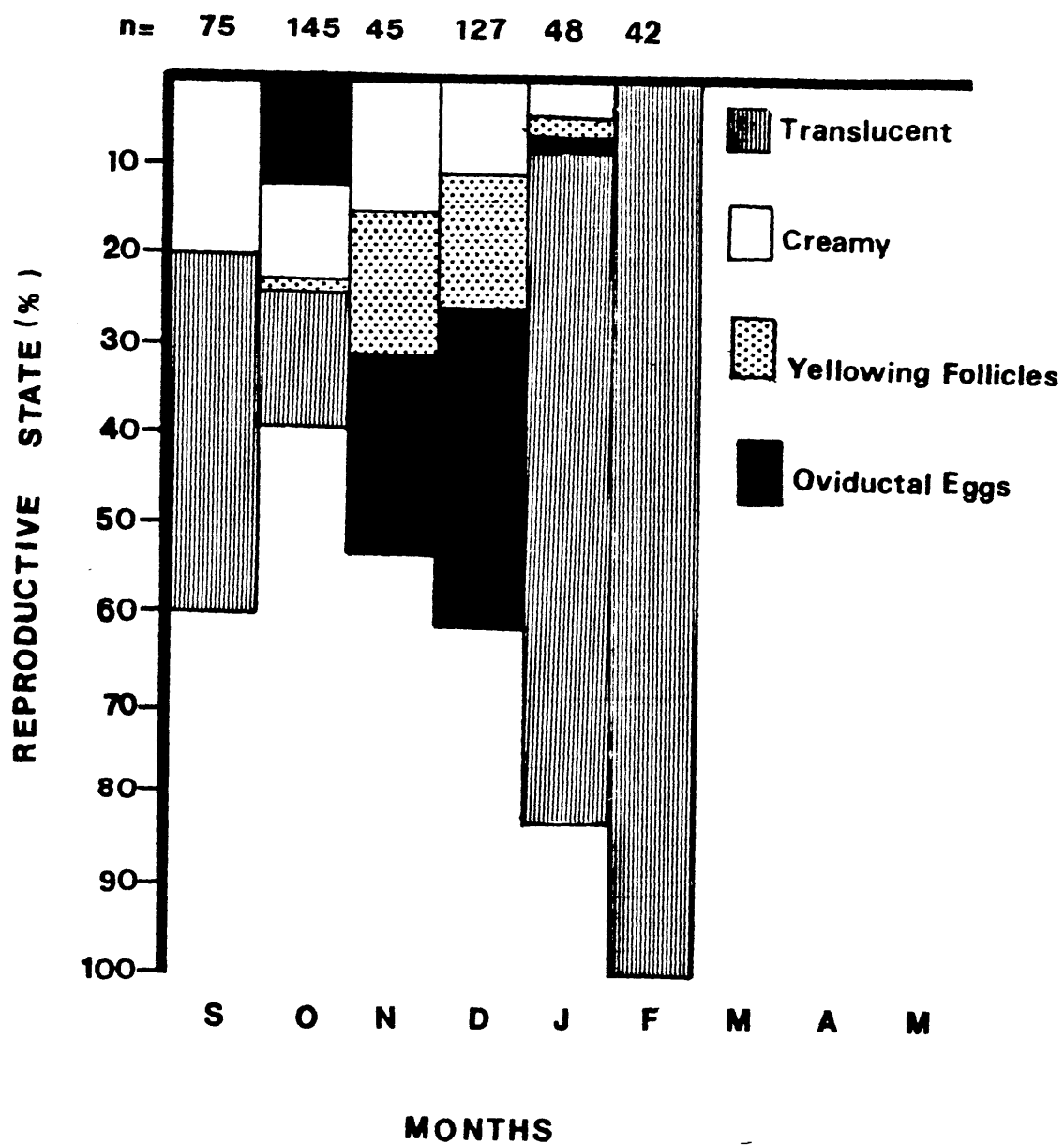


TABLE 13. Monthly distribution of ovarian follicles and oviductal eggs in adult *Lampropholis guichenoti*.

Months and years	Sample size	<u>Ovarian follicles</u> (mm)			<u>oviductal eggs</u>
		<u>translucent</u>	<u>creamy</u>	<u>yellowing</u>	
1983-84		0.1-1.9	2.0-4.0	4.1-7.5	7.6-10 mm
September	75	60 (80.00)	15 (20.00)	0	0
October	146	58 (39.73)	34 (23.29)	36 (24.65)	18 (12.33)
November	45	-	7 (15.56)	14 (31.11)	24 (53.33)
December	127	-	15 (11.81)	34 (26.77)	78 (61.42)
January	48	40 (83.33)	2 (4.17)	3 (6.25)	3 (6.25)
February	42	42 (100.00)	0	0	0
March	-	-	-	-	-
April	-	-	-	-	-
May	-	-	-	-	-

March. Most copulations were observed from October to November, a month or two before egg deposition. In the 1981-1982 season, gravid females with oviductal and/or enlarged ovarian eggs were collected mainly from October to February (Table 12, Fig. 25). At this time, the sizes of ovarian and oviductal eggs were also largest (Fig. 26). In 1981-1982 gravid females were found in five months whereas in the 1983-1984 season they were found only in four months and gravidity was at its peak in November and December (Table 13, Fig. 27). There is no strict synchronization of reproductive cycles for all females of *L. guichenoti*; occurrence of gravid females over such a long period shows that some females may breed early whereas others do so later.

Multiple clutches do not occur. The incubation period in *L. guichenoti* at Newholme (i.e. between oviposition and first appearance of neonates) at soil temperatures (50 mm below surface) of 21-25°C is between 56 and 74 days. From April onward of the 1981-1982 season, female *L. guichenoti* were found to have *corpora atretica* (degenerating ova) whereas this first happened as early as February in 1983 and 1984 (Tables 12, 13).

Soil temperatures during egg deposition and development in *L. guichenoti* at Newholme is 21.5 ± 2.77 (SD)°C in December, 25.68 ± 3.80 °C in January and starts to fall rapidly in February to 22.28 ± 2.85 °C when hatchlings start to appear.

Clutch size and frequency

Clutch size ranged from 1-4 ($\bar{x} = 2.4 \pm 0.84$ (SD), N=31) based on counts of enlarged vitellogenic follicles and was 1-3 ($\bar{x} = 2.26 \pm 0.55$; N=31) based on oviductal eggs. A year to year difference in clutch size showed only a significant difference in oviductal clutch size ($t = 2.58$, $P < 0.02$, $df = 64$; Fig. 28). Similar calculations did not show a similar significant result when ovarian clutch size was compared

between years (Table 14). Oviductal eggs of 31 adult females had a mean length of 7.27 ± 1.99 (SD) mm and a mean width of 4.3 ± 0.68 (SD) mm. Mean ratio of wet clutch weight to total weight (body and clutch weight) was 0.138 ± 0.2 (SD), $N = 27$, for mean female SVL of 42.6 mm.

Clutch size frequency as determined by counting oviductal eggs was: 1 egg, 5.3%; 2 eggs, 63.2%; 3 eggs, 31.5% in the 1981-1982 season. Similar results in the wet years 1983 and 1984 showed: no clutches of 1 egg; 2 eggs, 42%; 3 eggs, 56%; 4 eggs, 2% (Fig. 28). The number of eggs in a clutch seemed to increase linearly with increasing body size (SVL) ($r_s = 0.37$, $P < 0.05$, $df = 37$; (Fig. 29).

Body size, and age at maturity

Sexually mature females averaged 36.8 ± 0.41 (SE) mm (range 26-45 mm SVL, $N = 103$). Females of *L. guichenoti* are mature at an approximate SVL between 26.0 and 34.0 mm. From body size (SVL) growth data and results from a mark-recapture study, this length is usually acquired at an age of 8 to 9 months. The smallest reproductive female had a SVL of 34.0 mm and contained two enlarged ovarian eggs. The relationship of reproductive condition to body size (SVL) in *L. guichenoti* is illustrated in Figure 30.

The smallest young with distinguishable gonads was more than 24.0 mm SVL. The ratio of the minimum gravid female SVL to maximum SVL of females was 0.75 in the 1981-1982 sample. The ratio of hatchling SVL to minimum SVL of gravid females is 0.411 to 0.529.

The peak of gravidity coincided with increase in both rainfall and temperature (Fig. 24), but these correlations were not significant in either case; $r = 0.53$, $df = 5$, $P > 0.05$ and $r = 0.14$, $df = 5$, $P > 0.05$ respectively.

Fat bodies are greatly reduced by the end of summer and start to build up in autumn prior to the winter inactivity period (Fig. 31).

Figure 28. Yearly variation in clutch size in
L. guichenoti.

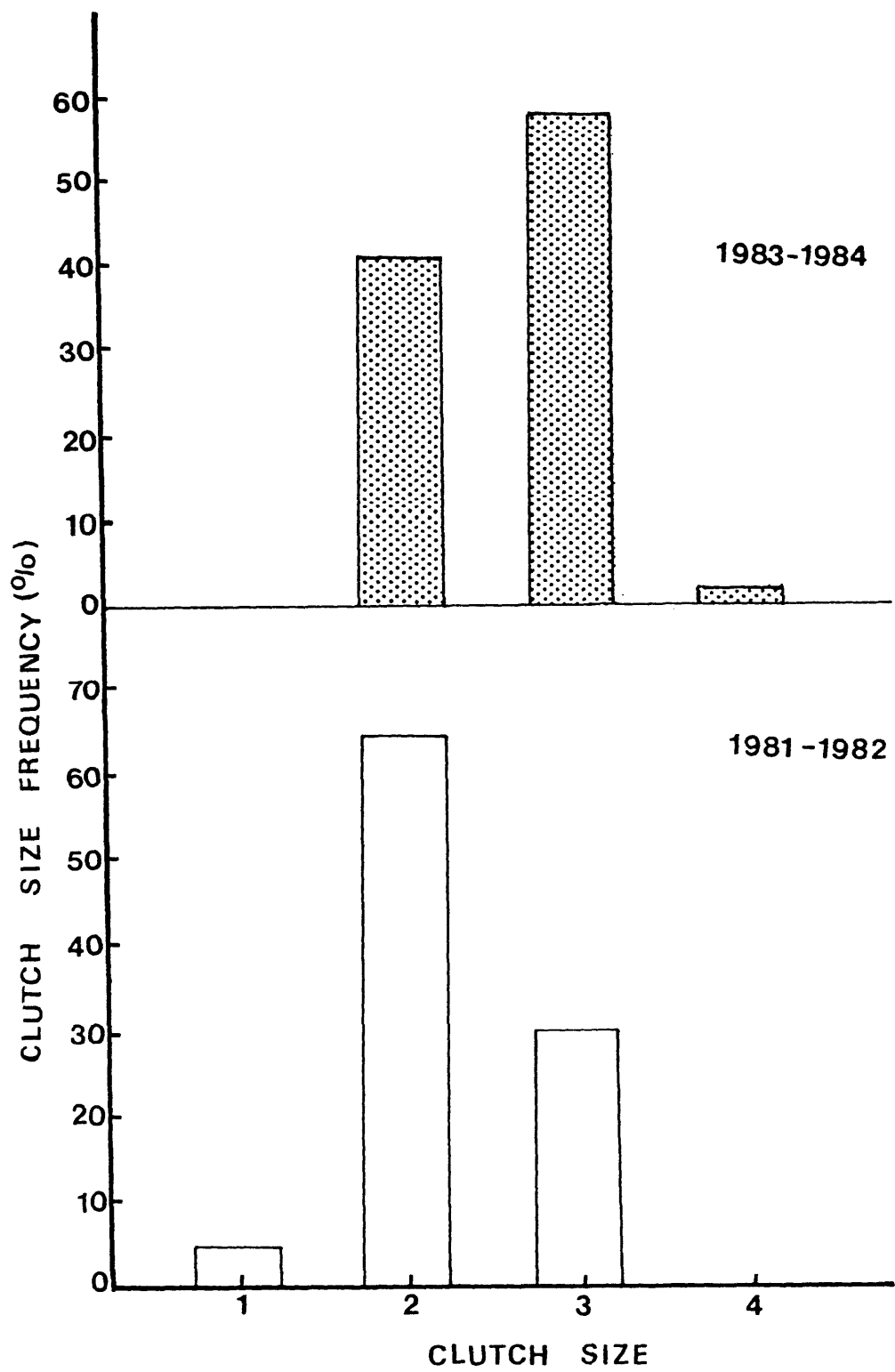


Figure 29. The relationship of clutch size and snout-vent length in *L. guichenoti* (N = 38).
Un-numbered dots represent a single female.

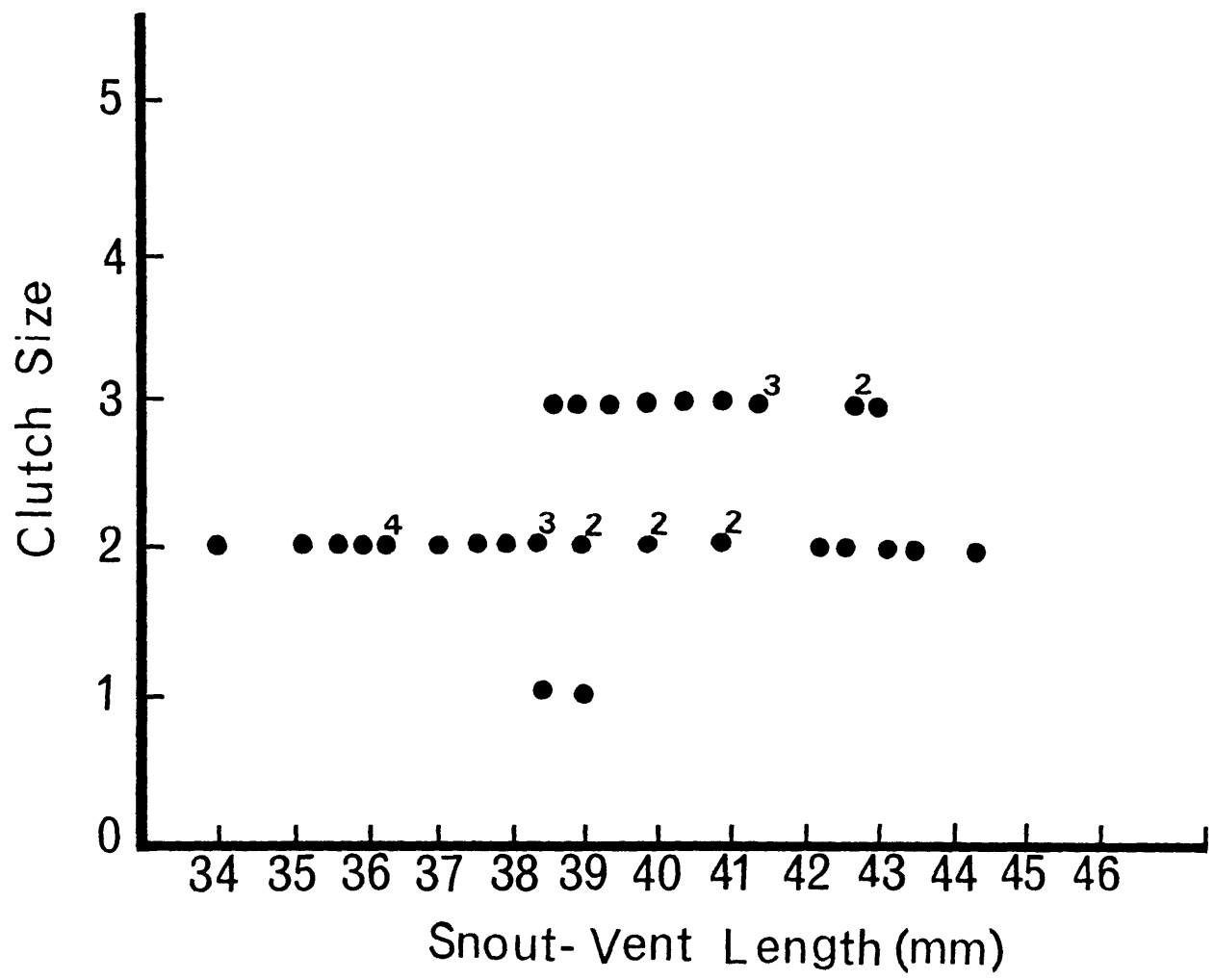


TABLE 14. Clutch size variation in *Lampropholis guichenoti*.

Years	Oviductal clutch size $\bar{X} \pm SD$	Ovarian clutch size $\bar{X} \pm SD$
1981-1982	2.26 \pm 0.55	2.41 \pm 0.81
1983-1984	2.61 \pm 0.55	2.50 \pm 0.58
t-test value	2.58	0.52
P	< 0.02	ns
df	64	64

Figure 30. Reproductive condition and snout-vent length in *L. guichenoti*. Reproductive condition: (1) immature, (2) mature, (3) old mature, (4) older mature. Each circle represents an individual specimen; for explanation of other symbols, see graph and text.

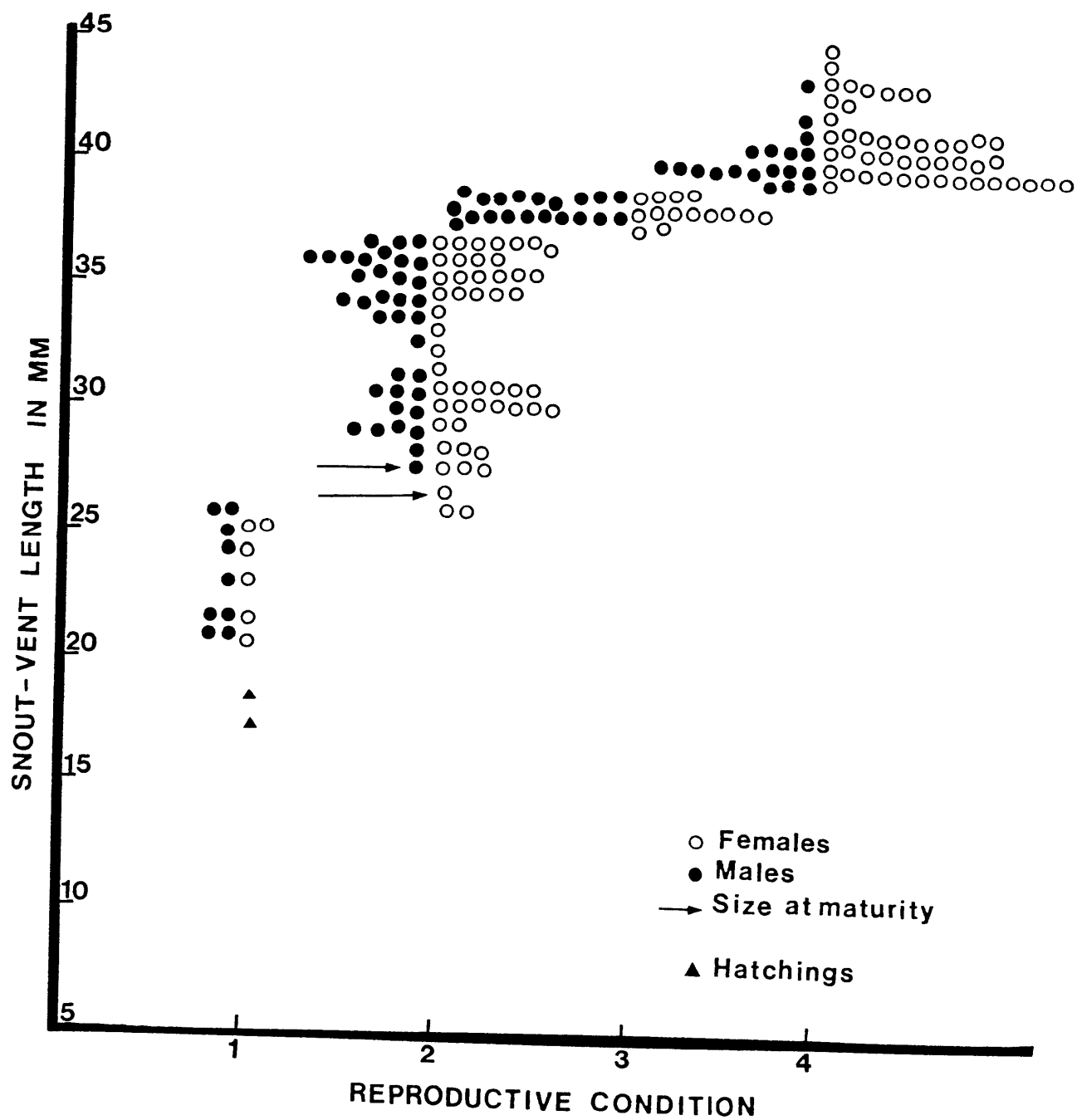


Figure 31. Seasonal variation in abdominal body fat mass in *L. guichenoti*. Males and females showed a similar cycle, hence data are pooled. Numbers represent sample sizes. Means are represented by horizontal lines and standard deviations by vertical ones.

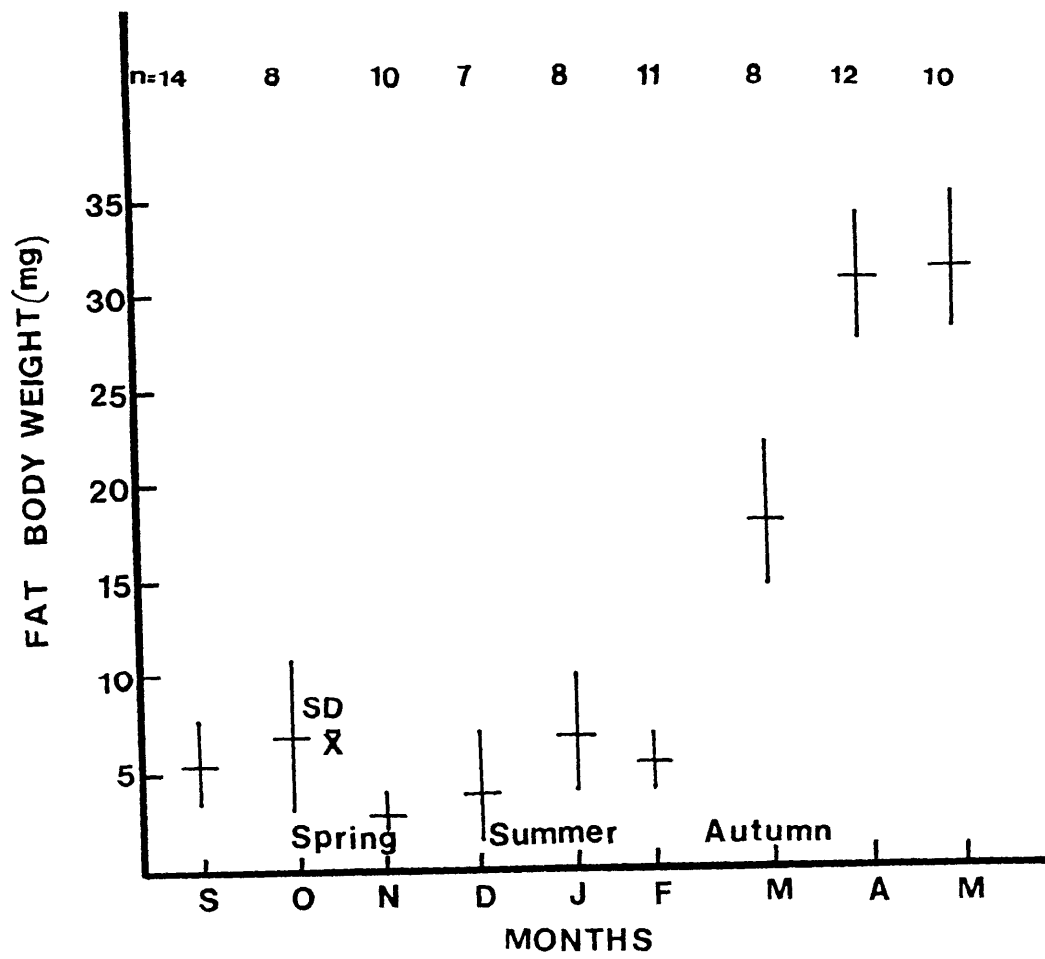


Figure 32. Secondary sex structure of *L. guichenoti*
based on proportions of adult males to adult
females in each monthly sample of the 1981-
1982 season.

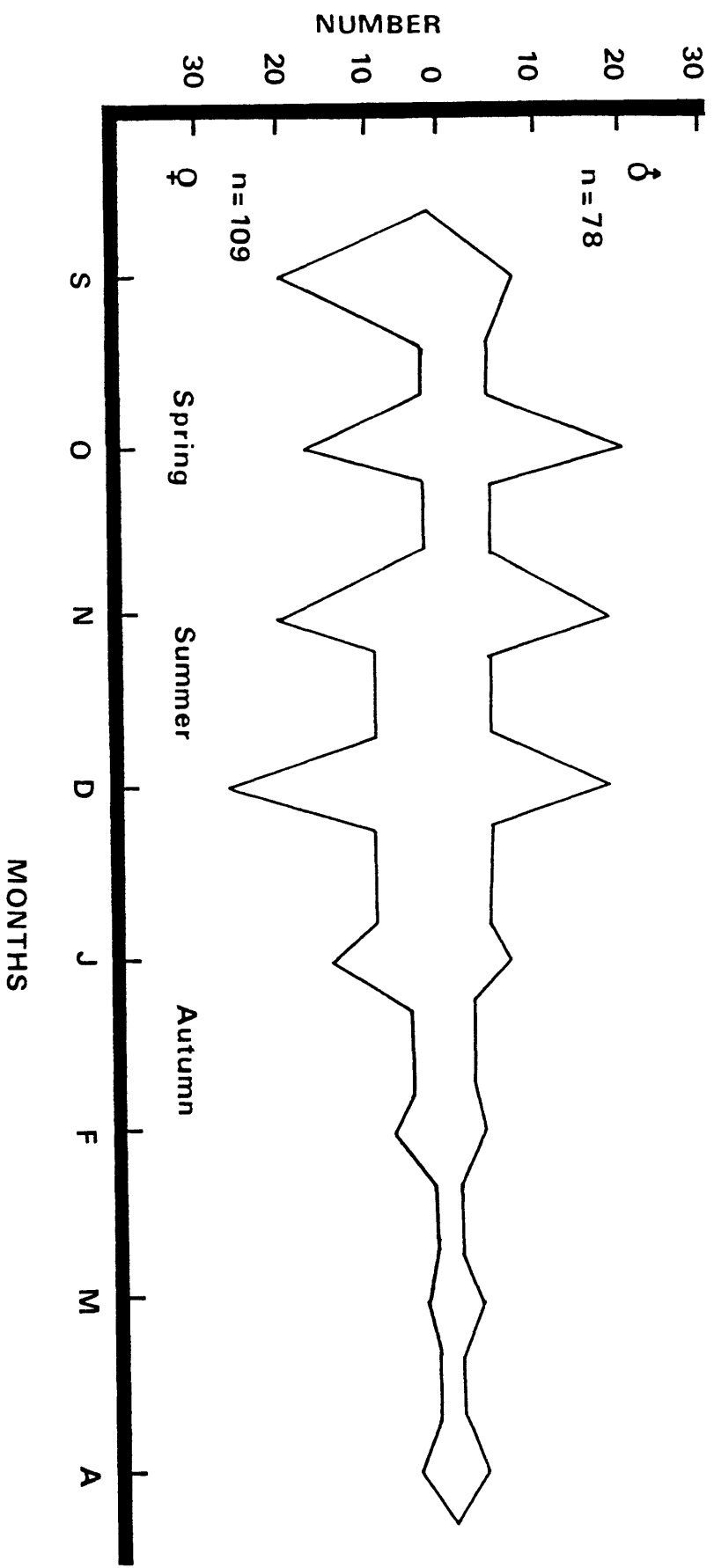
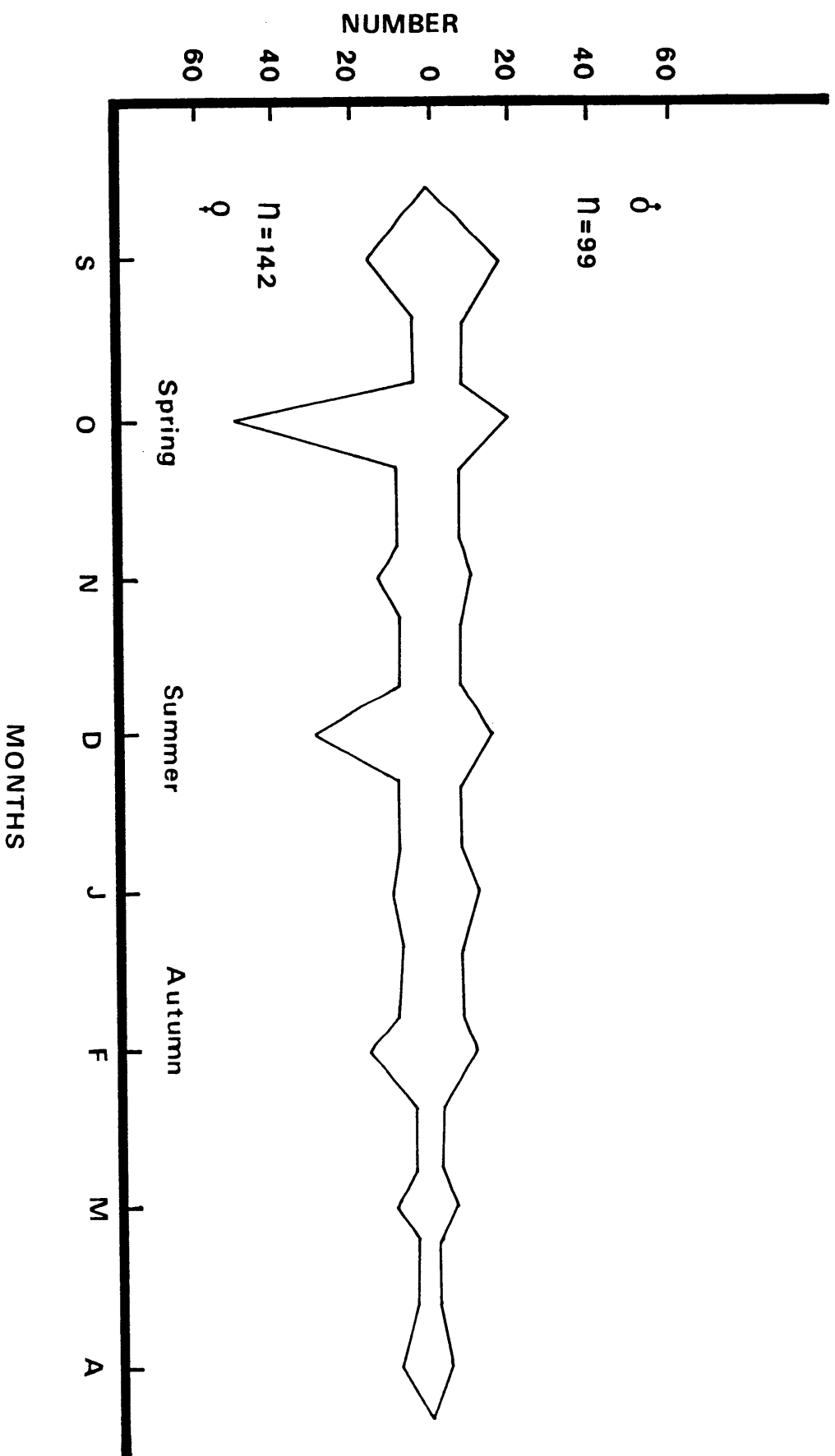


Figure 33. Secondary sex structure of *L. guichenoti*
based on proportions of adult males to
adult females in each monthly sample of
the 1983-1984 season.



Secondary sex ratio

There was a monthly deviation in sex ratio and in most cases this was in favour of females. This departure in secondary sex ratio towards females was more pronounced during summer and in particular during egg laying in *L. guichenoti* (Figs. 32, 33). However, the null hypothesis that there is no difference in monthly distribution of males and females could not be rejected for either the 1981-1982 season ($G = 7.40$, $df = 7$, $P > 0.5$) or 1983-1984 period ($G = 2.60$, $df = 7$, $P > 0.05$).

Soft morphology

The right ovary in *L. guichenoti* is situated slightly more anterior than the left ovary ($\bar{x} = 1.8 \pm 0.73$ (SD), $N = 37$). The right ovary is also more productive (produces larger number of eggs) than the left ovary ($t = 5.53$, $P < 0.001$, $df = 23$).

Timing of reproduction in H. decresiensis

The length of brumation in this species is similar to that of *L. guichenoti* and lasts until September. As with *L. guichenoti* that length was found to vary from year to year and perhaps depended on the weather conditions (temperature). Immediately after the winter inactivity period, ova mature in the ovaries, followed by ovulation in October. Gravidity was at its peak in November with a second peak in February (Fig. 24). New born appear first in December. *Hemiergus decresiensis* hatchlings have body size (SVL) ranging from 20.6 to 29.91 mm ($\bar{x} = 27.5 \pm 5.25$ (SD), $N = 17$) SVL and body weights from 0.12 to 0.48 g ($\bar{x} = 0.35 \pm 0.020$, $N = 17$). Gravid females were found in six months (Fig. 34). Some females breed early whereas others do so later. The occurrence of a second reproductive peak in February is characteristic of both species (Fig. 24) but ripened ova in the second period degenerate and do not form a second clutch of eggs or young (see also Table 15 and Fig. 34). Hence, multiple clutches do not occur in Newholme populations

Figure 34. Monthly frequency of reproductive state of female *H. decresiensis*. Sample sizes are given on each bar.

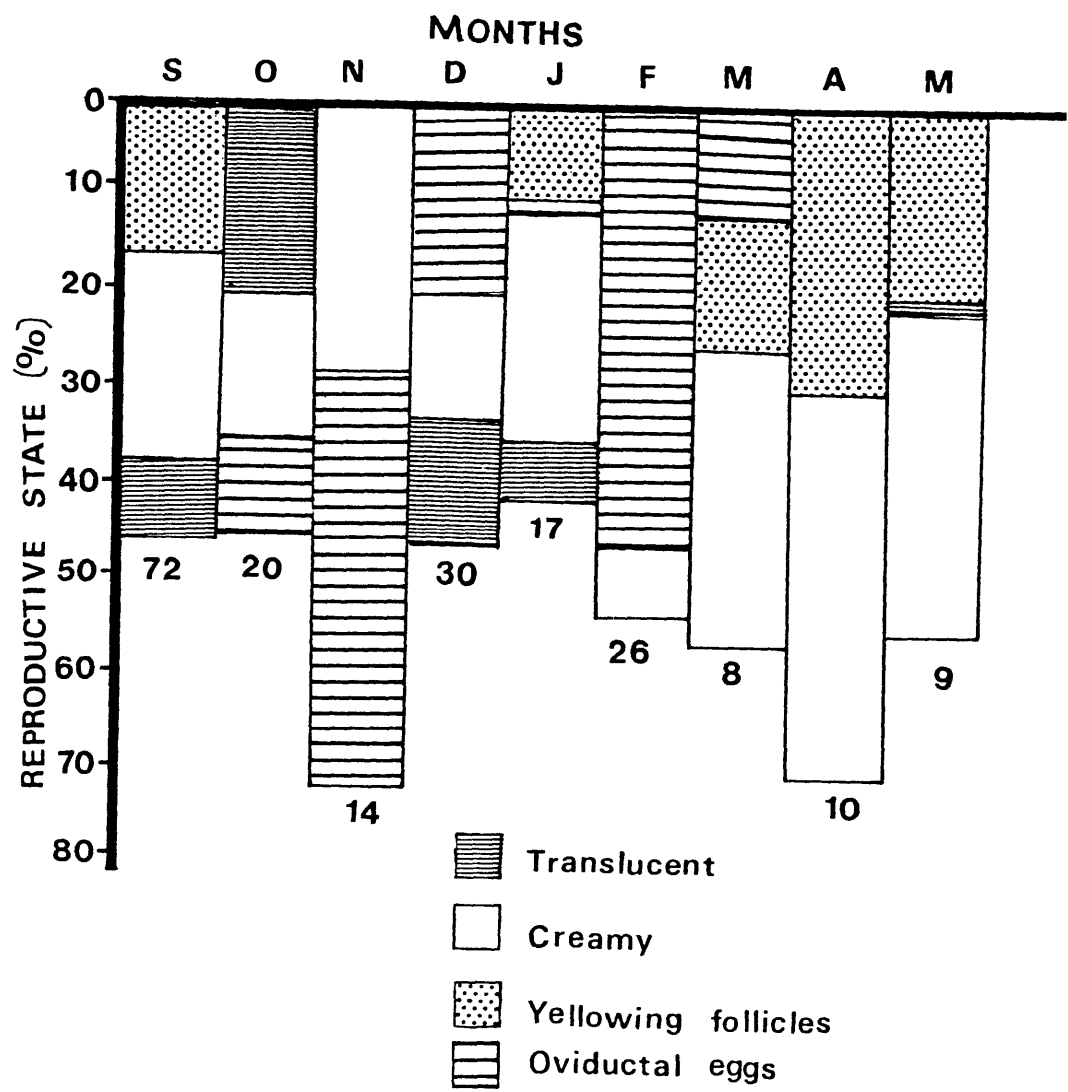
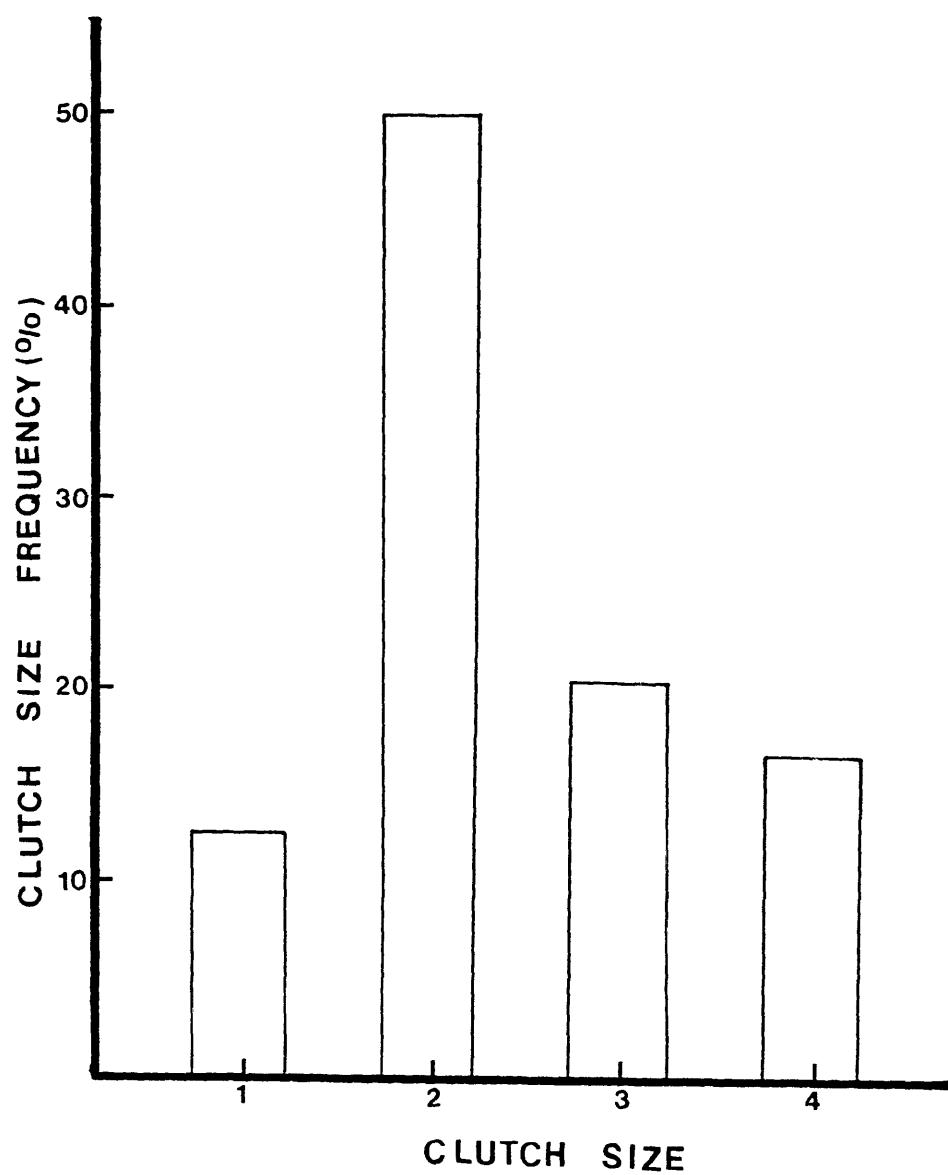


TABLE 15. Monthly distribution of ovarian follicles and oviductal eggs in sexually mature *Hemiergis decresiensis* (SVL \geq 45.0 mm).

Months and years	Sample size	Ovarian follicles (mm)			Oviductal eggs (or embryos) 7.6-10 mm
		translucent 1.0 - 1.9	Creamy 2.0-4.0	yellowing 4.1-7.5	
1981-82					
September	72	33(45.83)	27(37.50)	12(16.64)	-
October	20	4(20.0)	7(35.0)	-	9(45.0)
November	14	-	4(28.6)	-	10(71.4)
December	30	14(46.7)	10(33.3)	-	6(20.0)
January	17	7(41.1)	6(35.3)	2(11.8)	2(11.8)
February	26	-	14(53.8)	-	12(46.2)
March	8	-	5(62.5)	2(25.0)	1(12.5)
April	10	-	7(70.0)	3(30.0)	-
May	9	2(22.2)	5(55.6)	2(22.2)	-



of *H. decresiensis*. Based on information from time between ovulation and first appearance of newborn, gestation in *H. decresiensis* is rapid and lasts slightly over 30 days. Because of the secretive habits of this species, copulations were not observed.

Clutch size frequency

Clutch size frequency as determined by counting oviductal eggs was: 1 egg, 12.5%; 2 eggs, 50.0%; 3 eggs, 20.8%; 4 eggs 16.7% (Fig. 35). The number of young per brood did not increase significantly with increasing body size (SVL) ($r_s = 0.1$, $P > 0.05$, $df = 22$).

Based on number of embryos in the oviducts, clutch size in *H. decresiensis* ranged from 2 to 4 ($\bar{x} = 2.4 \pm 0.78$ (SD), $N = 21$), and from 1 to 4 ($\bar{x} = 2.3 \pm 0.88$ (SD), $N = 16$) when based on enlarged ovarian follicles.

Body size and age at maturity

Sexually mature females averaged 56.03 ± 3.83 (SD) mm (range: 29.9 – 67.1, $N = 65$). Female *H. decresiensis* mature at an approximate SVL between 30.0 and 45.0 mm SVL. Based on time interval between time when young first appear and time when juveniles are no longer recorded (see Fig. 15, Chapter 3, part 1) in the population, age at maturity in this species is attained at approximately 12 months. The smallest female with oviductal eggs or embryos was 45.0 mm SVL and the smallest female with creamy coloured ova in the ovaries was about 30 mm SVL.

The ratio of minimum gravid female SVL to maximum SVL of females was 0.666, whereas the ratio of SVL of the smallest hatchling collected in the field to the minimum SVL of females carrying embryos was 0.444.

Secondary sex ratio

There was a slight skewness in sex ratio in favour of females, i.e. 1:1.32 (Male: female).

Soft morphology

The right ovary is more anterior than the left ovary and the mean distance between the two was 3.18 ± 1.29 (SD) mm, $N = 27$. However, the left ovary is more productive in that there were slightly more embryos in the left oviducts than in the right ones but this difference was not significant ($t = 1.00$, $P > 0.05$, $df = 19$).

DISCUSSION

In the Newholme population of *L. guichenoti*, vitellogenesis begins in spring and ova rapidly increase in size from 1.9 mm to a mean of 4.0 mm, at which stage ovulation occurs. This concurs with data from Pengilley (1972) on Australian lygosomine skinks from Coree Flats. Such rapid ovarian development is typical of most temperate lizards having a long, severe winter and a short growing season (Fitch, 1973b). The timing of reproduction in *L. guichenoti* at Newholme may determine how much growth can occur during the short growing season (February to May) before the winter inactivity period. There is only one sexual cycle per season and only a single clutch is produced. The ova that form in late summer and autumn degenerate and are atretic. Individual females lay at different times during the season as indicated by Heatwole (1976). Milton (1980), having compared his natural history notes with Heatwole's (1976) findings suggested that the Queensland population of *L. guichenoti* may possibly have two clutches annually or that they may breed later. However, the detailed study of Queensland populations necessary to verify these suggestions remain to be carried out. Clearly, *L. guichenoti* have a reproductive strategy that falls into the early-maturing, single-

brooded strategy of Tinkle *et al.*, (1970). They are also discontinuous, seasonal breeders.

There is a correlation between the peak of reproduction and temperature and rainfall, but a cause-and-effect relationship has not been verified experimentally. Environmental factors are known to influence timing of reproduction in some other lizards (e.g. *Agama agama*, Marshall and Hooks, 1960). Heatwole (1976) provided a general review of examples of proximate environmental factors affecting reptile life histories. Rainfall seems to boost vegetation growth which may in turn affect arthropod production and availability. Some workers have shown how the advent of the rainy season and food abundance affect reproduction (Dunham, 1981). Ballinger (1977) measured relative food abundance and recorded reduced reproduction in *Erosaurus ornatus* in a year low in food (see also Mayhew, 1967 on *Uma*).

Chondropoulos and Lykakis (1983) demonstrated that dry conditions correlated with least production and wet ones with high production (see also Barbault, 1976). A similar trend was found in *L. guichenoti*. Females of this species were found to grow larger (also probably due to better survival), weighed more and produced larger clutches during wetter years (Chapter 3, part 1).

Under laboratory conditions Shine (1983a) found that the embryonic developmental period in *L. guichenoti* from Coree Flats, N.S.W. ranged from 35 to 73 days whereas Pengilley (1972) reported a period varying from 49 to 56 days. In the case of Shine (1983a) this was at temperatures between 20 and 26°C. Shine (1983b) classified the stage of *L. guichenoti* at oviposition to be between 25 and 31 which revealed that 55% of embryogenesis occurs *in utero* in this species. The present study

reports incubation times (between oviposition and first appearance of hatchlings) at soil temperatures (taken at 50 mm below surface) of 21 to 25°C to vary from 56 to 74 days.

Hatchlings are recruited in the population in February. At hatching, juvenile *L. guichenoti* are 44% of the length of the adult female mean body length but only 15% of the mean adult female body weight.

The ratio of wet weight of clutch to total weight (body + clutch weight) was 0.13 for females with a mean SVL of 42.6 mm. Shine (1980) gave a Relative Clutch Mass (RCM) value of 0.35 (mean SVL 43 mm) in *L. guichenoti*. RCM is related to foraging strategies, predator escape and habitat (Vitt and Congdon, 1978). It is also known that many additional ecological factors including differences in behaviour of lizards and resource abundance of their habitats influence RCM considerably (Schall, 1978; Congdon *et al.*, 1978).

The fat-body cycle described in the present study is characteristic of temperate lizards. Fat bodies increase before brumation, and are lowest at the time of breeding activity in spring, summer and part of autumn. This pattern of abdominal fat body storage and utilization is similar to that described in *L. guichenoti* from Corre Flats by Pengilley (1972). The importance of fat-body size to reproduction has long been demonstrated (Hahn and Tinkle, 1965; Smith, 1968). Derickson (1976b) also showed that lipids stored in *corpora adiposa* are the first reserves to be used for reproduction and maintenance.

Sex ratio in *L. guichenoti* in most months was slightly skewed in favour of females. This was most notable during ovulation and egg deposition. The aggregative behaviour of females about to deposit

eggs, make them more conspicuous at that time. Pianka (1970) and Schall (1978) noticed a temporary deviation towards males in lizards they studied during summer and attributed this to cryptic behaviour of females until egg deposition. In *Cnemidophorus deppii* Fitch (1973b) noticed that gravid females were slower and less elusive than adult males. Hence, he gave this as a possible reason why females were better represented in the samples he collected. Similar differences in behaviour of males and females of the same species was recorded in *Rana pipiens* in Minnesota by Merrell (1981).

Even though both *L. guichenoti* and *H. decresiensis* ovulate at the same time, *H. decresiensis* young appear two months earlier than the oviparous species *L. guichenoti*. There is only one sexual cycle in *H. decresiensis* and multiple clutches in one season do not occur. They are discontinuous and seasonal breeders and are in this way similar to *L. guichenoti*. Robertson (1981) did not record development of ova over winter in the Melville cave population of *H. decresiensis*. However, in Victoria this species ovulates a month later (November) compared with the October ovulation in the Armidale population. Young in Armidale appear as early as December, whereas Robertson (1981) recorded them only from February to early March in Victoria.

The peak of gravidity in *H. decresiensis* coincided with increasing temperature and rainfall. The rapid development of ova may be related to sperm storage in the oviducts. No copulations were observed in *H. decresiensis*, and this is because this lizard is highly secretive and has fossorial habits. However, Robertson (1981) reported mating in February and/or March which he said necessitated oviductal sperm storage during winter, until ovulation in spring.

Smyth (1974) removed tails from *Hemiergis peronii* in spring and showed that this inhibited development of ova. I collected no

H. decresiensis that had lost all its tail, and this may support Robertson's (1981) assertion that this species practices economy of autotomy (see also Chapter 3, part 2 of this thesis).

The importance of fat storage for reproduction has been shown in *Hemiergis peronii* and *Morethia boulengeri* (Smyth, 1974). The latter, like *H. decresiensis*, stores fat in the tail.

Like *L. guichenoti*, the secondary sex ratios of *H. decresiensis* were slightly skewed in favour of females. Differential behaviour or longevity and degree of crypsis between sexes may be some of the reasons why one sex is better represented in samples.

Unlike *L. guichenoti*, in which the right oviducts carry more oviductal eggs, *H. decresiensis* carries a slightly greater number of embryos in the left oviducts than in the right ones. In both species the right ovary is more anterior than the left one.

CHAPTER 5

MALE REPRODUCTIVE CYCLES

CHAPTER 5

MALE REPRODUCTIVE CYCLE

INTRODUCTION

Female reproductive cycles of skinks are now well known, but similar information on males is usually less detailed and less frequent in the literature (Fitch, 1970, 1982). Reproductive data are easier to gather for females compared to males which may require histological techniques for assessment of reproductive condition.

In the mid-1960's there was a general realization of the importance of the female reproductive system to life history studies (reviewed by Stearns, 1976, 1977). With the female reproductive system at the centre of life history studies, male reproduction in lizards was often mentioned only in passing and with reference to the female breeding patterns. Some workers studied the male reproductive system with reference to photoperiodism and temperature and how these control testicular activity cycles (Bartholomew, 1950, 1953; Fox and Dessauer, 1957; Fox, 1958; Saint-Girons, 1963; Mayhew, 1964; Licht, 1965; 1967a, 1967b; Marion, 1982). The bulk of the earlier studies on gonadal cycles of lizards are summarized by Porter (1972: 378-380).

Pengilley (1972) described histologically the male cycle of a number of skinks at Corre Flats, N.S.W. These included *Lampropholis guichenoti*. Robertson (1981) illustrated the male cycle of *Hemiergis decresiensis* at Melville caves, St. Arnaud Forest Station, Victoria. The present study describes the male sexual cycles of *L. guichenoti*

and *H. decreasiensis* inhabiting the Newholme area.

MATERIAL AND METHODS

Length and width of the testes (to the nearest 0.05 mm) were measured using an ocular micrometer. Monthly samples were also examined for size (largest width) of epididymides and nature of convolutions of semeniferous tubules. The distance between the right and left testis was recorded using vernier calipers, and the soft morphology of the male reproductive organs described.

Both testis size and weight produced a similar reproductive pattern. Results on testis size are reported here. Size was used as an indicator of testicular activity as these factors were found to be correlated by Pengilley (1972).

RESULTS

The male cycle of *Lampropholis guichenoti* is summarized in figures 24 (adjusted to body size) and 36. Testes are at their minimum size in spring. At this time semeniferous tubules are small and look evacuated (Fig. 37). Testes reach their maximum size in the summer months (December to February). Male gonadal growth is probably arrested during winter since samples taken just after brumation had individuals with small limp testes and small epididymides. The summer period of increased testicular activity is characterized by large, white, rounded testes covered with a fine mesh of blood capillaries and enlarged epidymides with heavily convoluted seminiferous tubules. The right testis is more anterior (2.16 ± 0.66 (SD) $N = 40$) than the left testis. Based on enlarged testes with heavily convoluted semeniferous tubules, the smallest male able to produce sperm was 27.2 mm SVL whereas the smallest mature male with large vascular testes was 32.8 mm SVL. Hence, sexual maturity in

Figure 36. Annual reproductive events in *Lampropholis guichenoti* males (above) and females (below). The left lower ordinate shows the different reproductive condition as; 0-1 = quiescent; 1-2 = initiation of reproduction and 2-3 = reproductive period. Each bar (above) shows range (vertical) mean (horizontal) and standard deviations (rectangles) of the testis length. Numbers denote sample sizes.

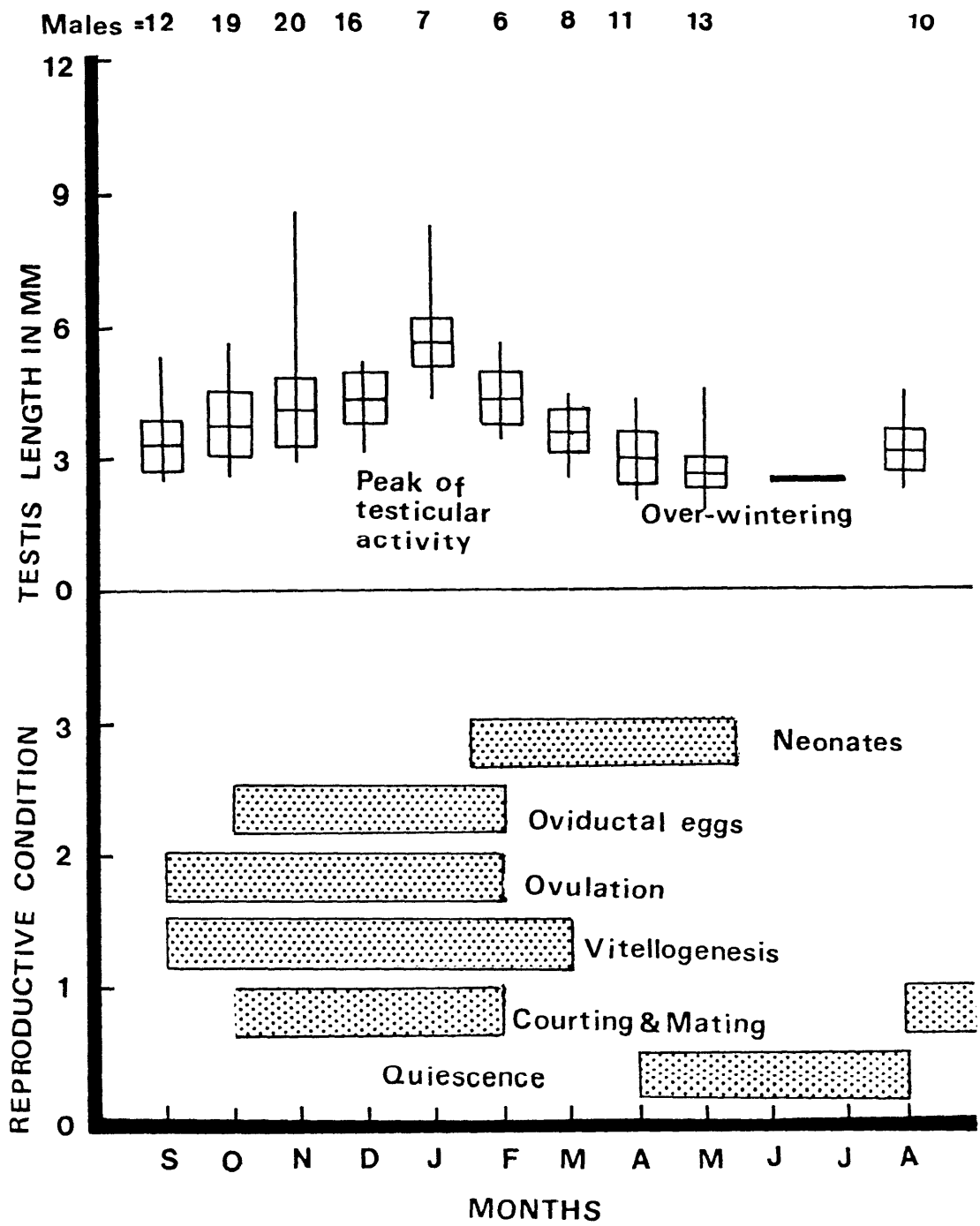
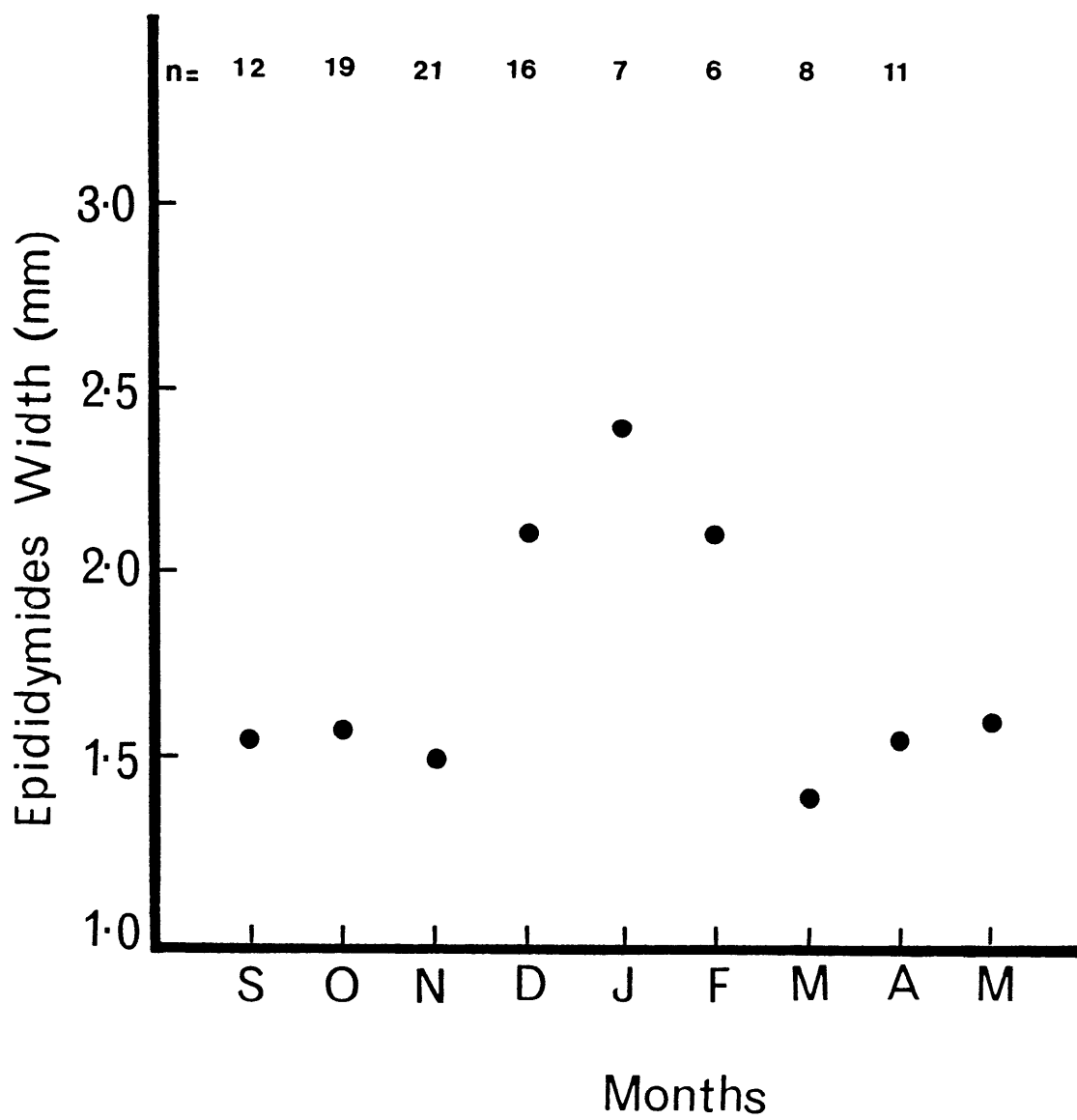


Figure 37. Monthly variation in mean size of epididymides of sexually mature *L. guichenoti*. Numbers represent sample sizes.



L. guichenoti males is attained between 27.2 and 32.8 mm SVL. Among 56 sexually mature adults examined, mean testes size (average of left and right testes) is 2.7 ± 0.94 (SD) width and 4.27 ± 1.6 mm length.

The male cycle coincided with increase in amount of rainfall and rise in ambient temperature. However, this relationship was not statistically significant in either case; $r = 0.51$, $df = 7$, $P > 0.05$ and $r = 0.34$, $df = 7$, $P > 0.05$ respectively. The peak of testicular activity occurred at the peak of female reproductive activity (Fig. 24, Chapter 4) but this relationship showed a weak correlation ($r = 0.12$, $df = 5$, $P > 0.05$).

Testis size increased with increase in body size ($r^2 = 0.67$, $P < 0.01$, $df = 29$ ($Y = -0.27 + 0.11x$) (Fig. 38). Courting and mating was observed in August to February (Fig. 36).

The male cycle of *Hemiergis decresiensis* is described in figure 24 of Chapter 4. The cycle is similar to that of *L. guichenoti* males in that testes size is at a minimum in spring and a maximum when the females are at their reproductive peak. May seems to be the month for drastic changes in *H. decresiensis* testis; the testes collapse, become limp and small and the semeniferous tubules are smaller. Based on 53 sexually mature adult males, mean testes size (average of left and right testes) is 3.15 ± 0.32 (SD) width and 4.8 ± 0.58 mm length. The right testis is forward of the left testis ($\bar{x} = 3.46 \pm 1.43$ (SD), $N = 17$).

The male cycle coincided with increase in rainfall and rise in temperature (Fig. 24, Chapter 4). Testis size increased with increase in body size (SVL): $r^2 = 0.61$, $P < 0.01$, $df = 17$ ($Y = -1.97 + 0.12x$) (Fig. 39). Courting and mating could not be observed in the field because *H. decresiensis* rarely ventures from cover and is secretive.

Behaviour of males

In both species both sexes look alike with no obvious external feature differentiating the two sexes. However, based on autopsied

Figure 38. Relationship of testis length to body size (SVL) of *L. guichenoti*. The regression equation is $Y = -0.21 + 0.11x$ ($P < 0.01$).

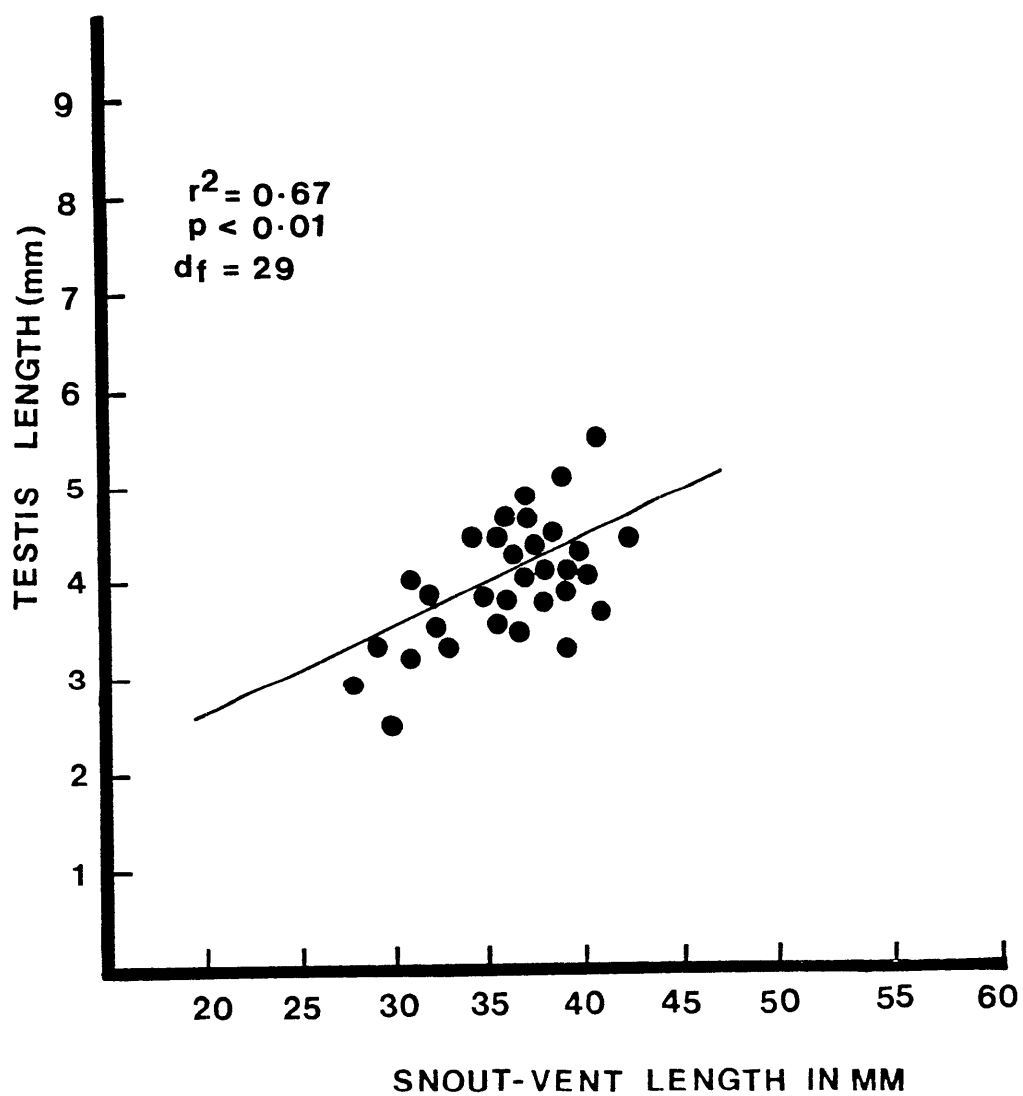
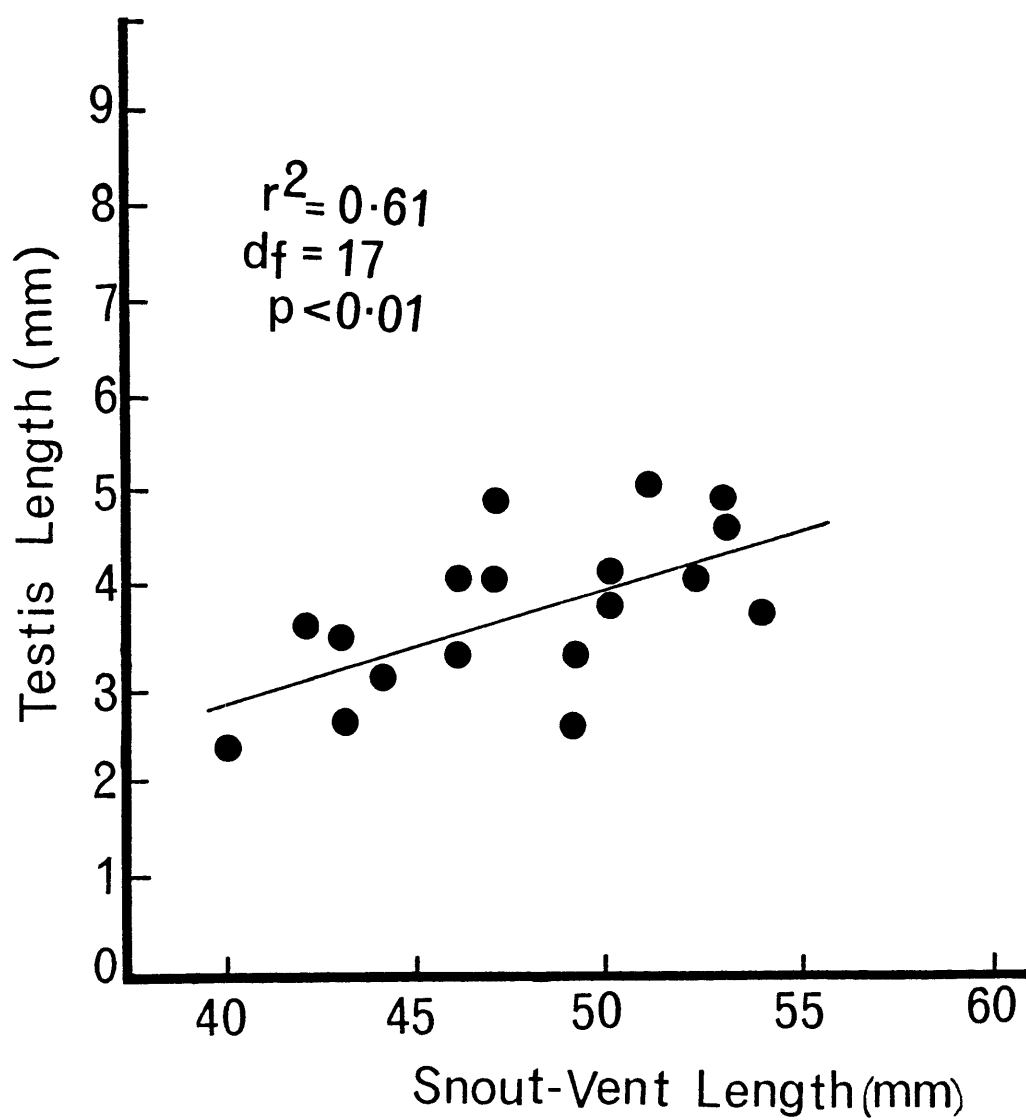


Figure 39. Relationship of testis length to body size (SVL) in *H. decresiensis*. The regression equation is $Y = -1.97 + 0.12x$ ($P < 0.01$).



individuals females are larger than males and this is more pronounced in *H. decresiensis* (see Chapter 3 and tables 6 and 7). Females of *L. guichenoti* tend to aggregate during egg deposition in summer (November to December) and hence are better represented in monthly samples during this time of year (see also Figs. 32, 33, Chapter 4).

DISCUSSION

The present study has described the male reproductive cycles of *L. guichenoti* and *H. decresiensis*. The seasonal testicular cycles based on greatest length expressed as a ratio of SVL (testis index) are very similar in both species. Sexually mature males of both species emerge from brumation (August to September) with testis size at or near minimum. The male cycles of these species resemble those described by Pengilley (1972) in his study of lygosomine skinks, including *Leiolopisma guichenoti* populations at Corre Flats. Pengilley (1972) found that most testes do not contain sperm until towards the end of December, which means that mere increase in testis size may indicate nothing concerning the period of maximum spermiation (but see also Towns, 1975). Present data show that *H. decresiensis* had a slightly greater testis size to SVL ratio than was the case for *L. guichenoti*. Mating in *L. guichenoti* was observed in spring and resembles a "prenuptial" pattern (Volsøe, 1944; Lofts 1969; Licht, 1982; Garstka *et al.*, 1982 and Saint-Girons, 1982). This is a typical breeding pattern among seasonally breeding species where gamete maturation occurs as a single discrete event during or immediately prior to breeding. Inasmuch as growth is arrested during winter dormancy, the cycle resembles the "postnuptial" type (Garstka *et al.*, 1982).

The reproductive cycle of *Hemiernis decresiensis* at Newholme is similar to that of a *H. decresiensis* population in Victoria (Robertson, 1981). Robertson (1981) also found that the Victorian population was similar to *H. peronii* studied by Smyth (1968). Both these authors indicated that copulation in both species occurred in autumn which necessitated sperm storage in the female oviducts (Smyth and Smith, 1968). In *Agkistrodon piscivorus*, spermatozoa are stored in male reproductive organs during winter (Johnson *et al.*, 1982).

Testis size varied seasonally and tended to parallel egg production in females. Baker (1947) reported a similar incidence in the skink *Emoia cyanura* from Espiritu Santo in the New Hebrides.

Soft morphology of *L. guichenoti* females and males resemble that of *Leiolopisma suteri* inhabiting northeastern New Zealand (Towns, 1975). In both *H. decresiensis* and *L. guichenoti*, the right testis lies forward of the left one. The epididymis is long, and extends back to the kidney, where it straightens to form the vas deferens, which leads to the urinogenital papilla (Towns, 1975).

In most skinks there are no external features that differentiate the sexes, but most studies have reported sexual dimorphism in body size (SVL) with males in most cases being smaller than females. In *Mabuya striata* sexually mature breeding males have coloured gulars, and a distinct colour dimorphism exists in *Mabuya quinquentaeniata* (Simbotwe, 1980).

The male reproductive cycles of both species coincide with periods of increasing rainfall and rising temperature but this relationship was not statistically significant. Many authors have studied the influence of endogenous and external factors on the testicular activity of reptiles (Bartholomew, 1953; Johnson *et al.*, 1982; Licht, 1982; Marion, 1982; Saint-Girons, 1982). Much of the earlier work on the relationship of the male cycle to endogenous (neurological

and hormonal) and exogeneous (temperature, rainfall, photoperiod and food) factors are summarized by Porter (1972: 378-380).

Testicular recrudescence (TR) in the presently studied species closely parallel environmental temperature changes and the advent of the rainy season. Licht (1967a) showed in *Anolis carolinensis* that temperature acts more directly in modification of TR and that photoperiodism acts only to facilitate the temperature response. Important findings of the present and other studies are that the male cycle parallels the female cycle, increase in testes size does not necessarily correspond with the peak of spermiation, and testicular cycles are correlated with environmental temperature. An emphasis on life-history studies and the female reproductive cycle, has masked the importance of the male sexual cycle. It is hoped by this study that in future more detailed study of the male cycle of skinks will be carried out.

CHAPTER 6

SIZE STRUCTURE OF THE POPULATION

CHAPTER 6

SIZE STRUCTURE OF THE POPULATION

INTRODUCTION

Demographers show interest in body size frequencies in populations because they reveal something about growth patterns and potential increases or decreases in population size over time and indicate the rate of turn-over, i.e. how birth and death interact in a particular population (see Chapter 1). But because of inherent difficulties, information on population structure of lizards is scarce in the literature and most reports on field studies of lizards rarely make mention of it. Some of these difficulties involve differences in behaviour between species, sexes and between young and adults. Fitch (1973b) asserted that these differences may cause differential susceptibility to capture so that any sample obtained is somewhat biased. Comparisons between species and within species with respect to population structure are confounded with difficulties due to growth rates that may vary greatly in time and space, between localities or between individuals. Size classes result from discontinuous reproduction, rate of turn-over and longevity. An estimate of population turn-over and longevity is based on learning about survival and movements of individuals through marking of individuals as hatchlings (see Chapter 2, part 2).

Reproduction determines to a large extent the population structure. The body size frequencies remain stable only if reproduction goes on continuously at a constant level. But these are rare situations and in the majority of lizard populations reproduction

is variable. Some populations show annual breeding (see Chapter 4) and most of these are of temperate distribution whereas among tropical lizards, long breeding seasons, sometimes covering the whole year are common (Fitch, 1973b). Because of this variability in breeding habits of some lizards, Fitch(1973b) demonstrated among 21 populations he sampled that no two were alike in both structure and stability.

This chapter is devoted to learning about body size frequency in *Lampropholis guichenoti* and *Hemierngis decresiensis* populations in Armidale. Pengilley (1972) discussed briefly body size frequency in *Lampropholis* (formerly *Leiolopisma*) *guichenoti* but never discussed the topic in relation to any general theory. No studies to my knowledge, have addressed this topic for *H. decresiensis*.

MATERIAL AND METHODS

In order to study body size frequency and variation in the Newholme populations of *L. guichenoti* and *H. decresiensis*, monthly samples of lizards were classified for each sex according to body size (age). In *L. guichenoti* this classification resulted in 11 different size classes of 2.9 mm intervals each; i.e. (1) 15.0-17.9, (2) 18.0-20.9, (3) 21.0-23.9, (4) 24.0-26.9, (5) 27.0-29.9, (6) 30.0-32.9, (7) 33.0-35.9, (8) 36.0-38.9, (9) 39.0-41.9, (10) 42.0-44.9 and (11) 45.0-47.9 mm SVL.

Because *Hemierngis decresiensis* were rare at all times in 1981-1982 only limited data were obtained. Because of floods only 10 adult females, 1 adult male and 1 subadult were collected for the entire period of 1983-1984. This precluded detailed analysis for this species.

According to a mark-capture-recapture program, individuals of size classes between 1 to 7 are less than 12 months old, those between 8 and 9 size classes are 12 to 24 months old and those of 10 and 11 size classes are over 24 months old.

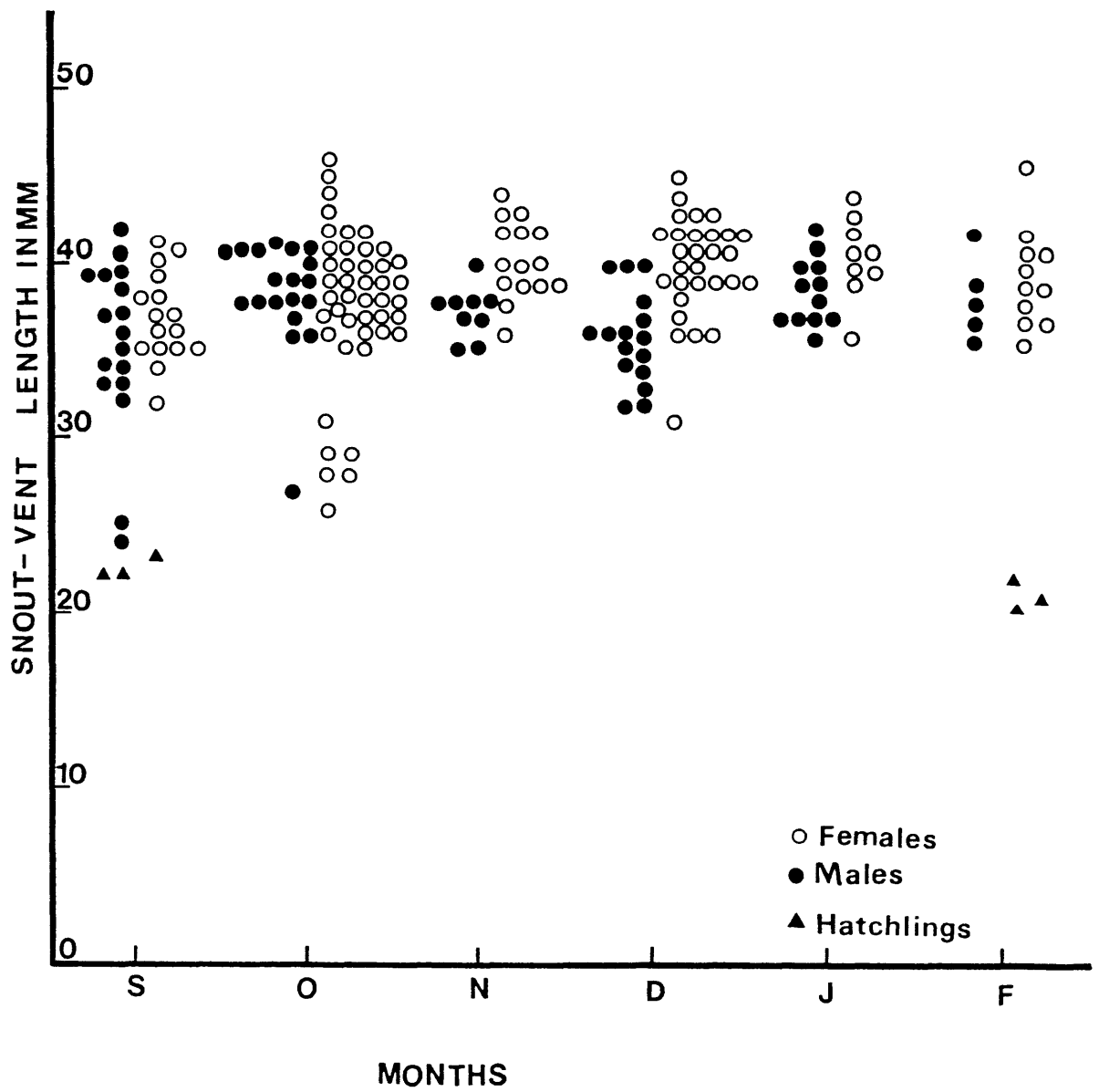
In order to avoid over-collecting, individuals collected for reproduction and body size studies were sampled from two different areas i.e. sandy creek at the back of Mount Duval (1981 and 1982) and an area 1 km southeast of the Newholme laboratory (1983-1984).

RESULTS

Body size frequency in *L. guichenoti*

Monthly changes in body size (SVL) are provided for hatchlings, subadult and adult males and females collected and examined from 1981 to 1984. The size (SVL) distribution profile (Fig. 40) reveals that hatchlings are recruited in the population in February. They grow for 4 months (February, March, April and May) before over-wintering. They come out of hibernation in August or September without having undergone much additional growth. This is shown by the broad overlap in size (SVL) between the February group of hatchlings (1983) and the September group in the second growing season (1984) (Fig. 40). This size distribution pattern is similar to that described for this species in the 1981 to 1982 study (see Chapter 3, Fig. 14). There is monthly and seasonal variation in body size (Fig. 41 and Table 16). A monthly analysis of body size frequency shows that females are larger than males during November ($t = 4.65$, $P < 0.001$, $df = 31$), December ($t = 2.11$, $P < 0.05$, $df = 43$) and January ($t = 2.37$, $P < 0.05$, $df = 29$) but not in September, October and February (Table 12).

Figure 40. Size structure of *L. guichenoti* in the 1983 and 1984 season. Open circles represent individual females and closed ones individual males. Triangles represent individual hatchlings.

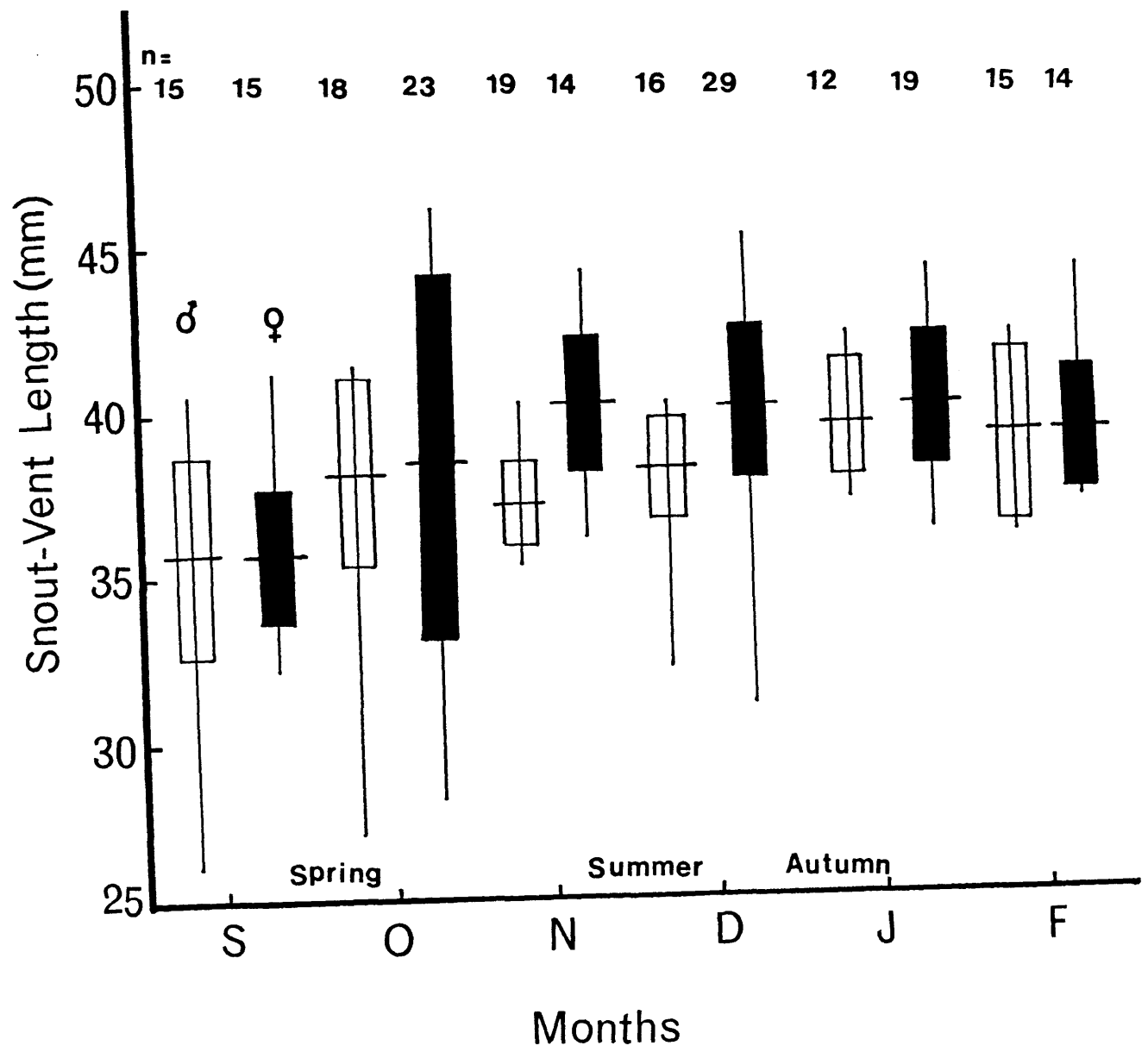


A seasonal distribution of body sizes of adult males and females showed a similar increasing trend from spring through summer to autumn. Spring samples had individuals ranging from 26.0 to 46.0 mm SVL, whereas summer samples recorded a range of 31.0 to 45.0 mm SVL and autumn recorded 36.0 to 44.0 mm SVL (Fig. 41).

An analysis of body size structure (Fig. 42) shows a size profile of subadults in their second growing season (size classes 3 and 4) and of adults for the years 1981 and 1982. Generally, the distribution of body size frequencies is broader during spring (September to November), and is narrowest in autumn (February to April) when only individuals over 30.0 mm SVL occur. In this species, individuals of the aforesaid size are about 9 months old. Age estimates are based on capture-recapture studies on individuals marked as hatchlings. Looking at the way mean body size distribution graphs are constructed in Figure 41, it appears as though both sexes are distributed uniformly ($\chi^2 = 1.33$, $P > 0.05$, $df = 5$). There are, however, some differences in average monthly body size (Table 16).

In September, individuals of both sexes ranged from 24.0–45.0 mm SVL. Among males, individuals ranging from 24.0 to 31.9 mm made up only 15% of the population, whereas those ranging from 32.0 to 36.9 mm made up 34%, and those from 37.0 to 42.9 mm 17%. Individuals of 2 years and over, i.e. 43.0–45.0 mm made up 34% of the monthly sample. In females, individuals between 24.0 and 31.9 constituted 24% of the population, those from 32.0 to 36.9 mm comprised 15%; the majority of individuals (53%) were from 37.0 to 42.9 mm. The 43.0 to 45.0 mm group were in the minority and comprised only 8% of the total monthly sample of females. Among males, individuals of 32.0 to 36.9 mm SVL

Figure 41. Seasonal body size variation among adult *L. guichenoti* in the 1983-1984 season. Vertical lines are ranges, horizontal ones are means and rectangles represent standard deviations of the mean. Numbers denote sample sizes.



were in the majority together with those ranging from 43.0 to 45.0 mm. In females the 37.0 to 42.0 mm SVL class was predominant.

In October the range of body size frequency was larger than in September. This could be because of differences in times of emergence from brumation by various age size groups (see Fig. 42). Individuals collected in this month ranged from 21.0 to 45.0 mm. Among males, the majority of individuals were between 32.0 to 42.0 mm (60%) with individuals between 24.0 to 29.9 mm accounting for 13% and those between 42.9 to 45.0 mm making up 20% of the total males examined in October. Individuals ranging from 21.0 to 26.9 mm made up only 7% of the total males. Among females, no individuals below a class of 4 or beyond a class 9 were recorded. The majority of individuals were between 32.0 and 42.0 mm, a situation analogous to males, but among females this size class range comprised 80% of the total animals recorded in October. Individuals in the 24.0 to 29.9 mm SVL size class made up only 20% of the animals examined.

The November sample of both sexes contained only individuals between 21.0 and 44.9 mm SVL. The range of body size was greater for females (21.0 to 44.9 mm) than for males (24.0 and 41.9 mm).

Males in the 21.0 to 26.9 mm classes (younger than 9 months) accounted for 10% whereas those of 27.0 to 32.9 mm (between 9 and 12 months old) made up 22% of the total animals examined. The majority of animals (68%) were between 33.0 and 38.9 mm or 12 to 18 months old. These same age/size classes comprised the majority (60%) of females collected in November. The 21.0 to 26.9 mm size class was represented by 20% of the individuals examined, whereas the 27.0 to 32.0 mm group accounted for 14%, and the 39.0 to 44.9 mm group made up of a mere 6%. The last size class was made up of individuals 2 years of age or older.

Beginning in December the range in body size of both male and female *L. guichenoti* narrowed and all individuals were either sexually mature or nearly so. The sizes of females ranged from 24.0 to 44.9 mm and those of males ranged from 24.0 to 41.9 mm. Although the majority (50%) were between 36.0 and 41.9 mm, December samples had a majority of individuals slightly older (size classes 8 to 9) than did November samples (majority in size classes 7 to 8). In December, the male size group falling between 30.0 to 35.9 mm made up 37% of the examined individuals whereas that between 24.0 and 29.9 mm comprised 13%.

Animals between body sizes 36.0 and 41.9 mm made up the majority (52%) of females examined in the December sample. The 24.0 to 29.9 mm group made up 8% of the females whereas those between 30.0 and 35.9 mm SVL accounted for 18%. The older group (42.0 to 45.0 mm) constituted 22% of the total females examined.

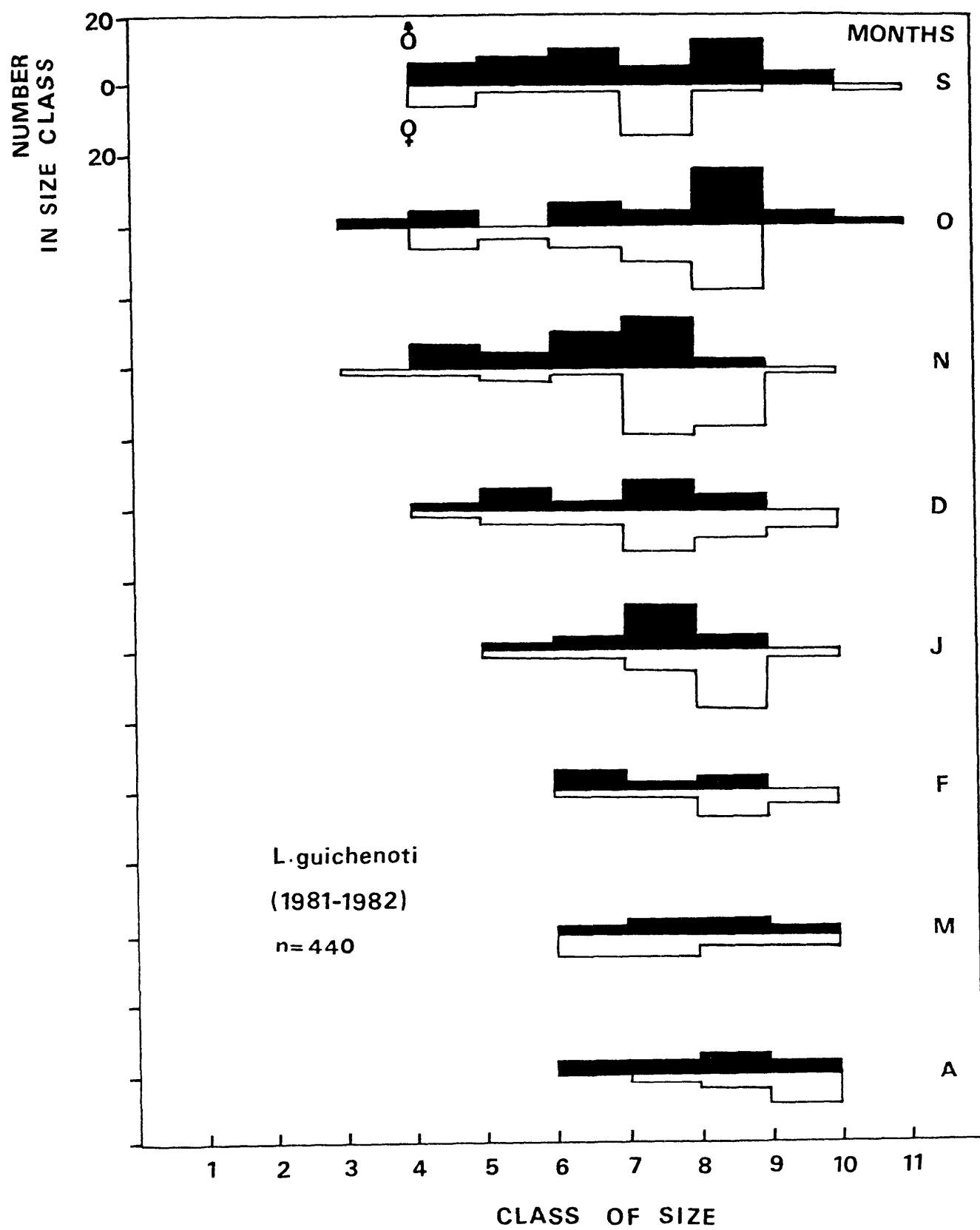
In January the range in body size widened because of animals in their second growing season reaching maturity. Body size for both sexes ranged from 27.0 to 44.9 mm. During this month, 12% of the males examined were of individuals ranging from 27.0 to 32.9 mm. Individuals measuring between 33.0 and 38.9 mm were in the majority and made up 66% of the total males examined, whereas the larger group (39.0 - 44.9 mm) comprised only 22%. Among females, 66% of the total were individuals of an older category, ranging between 39.0 and 44.9 mm. Hence, in January, individuals between 12 and 24 months old were in the majority. Twenty-five percent of the total females examined in January were between 33.0 and 38.9 mm, whereas those measuring between 27.0 - 32.9 mm made up of only 9%. Clearly, there was an increasing trend towards a greater representation of larger, hence older, animals in these samples.

The frequency distribution of body sizes among adult *Lampropholis guichenoti* was even narrower in February and only had individuals between 30.0 and 44.9 mm. This result revealed an exclusion of the smaller (21.0–29.7 mm) as well as the larger and older (42.0–47.9 mm) individuals. This situation remained similar both in the 1981 and 1982 samples of March and April (Fig. 42). It is, however, interesting to note that hatchlings are recruited in the population beginning in February (Fig. 40). Young males represented the largest category (42%), i.e. individuals measuring between 30.0 and 35.9 mm. Individuals measuring 33.0 to 38.9 mm comprised 25% of the total males examined in February whereas the slightly larger (hence older) individuals (36.0 – 41.9 mm) made up 33% of the total sample. The size distribution for females was broader and included individuals between 30.0 and 44.9 mm. The largest category (50%) of females were of larger size (older), i.e. 36.0 to 41.9 mm, and the largest single class of females (39.0–44.9) accounted for 25%. In February those females that measured between 30.0 and 35.9 mm constituted 12% of the female population whereas those within the range of 33.0 to 38.9 mm made up 13%.

In March, males and females both tended to show an even frequency distribution of body sizes. Among males examined, 30.0 to 35.0 mm individuals comprised 38% whereas those measuring between 33.0 and 38.9 mm and 36.0 and 41.9 mm SVL each comprised 25% of the total males sampled in March. The classes of larger (older) individuals (42.0–47.9 mm) made up only 12% of the total sample.

The April sample had a body size frequency distribution similar to that of the March sample, with the exception that females were not represented in the 30.0 to 35.9 mm size class. Males were nearly uniformly distributed with various age/size classes represented as

Figure 42 . Body size distribution in *L. guichenoti*
in the 1981 - 1982 season.



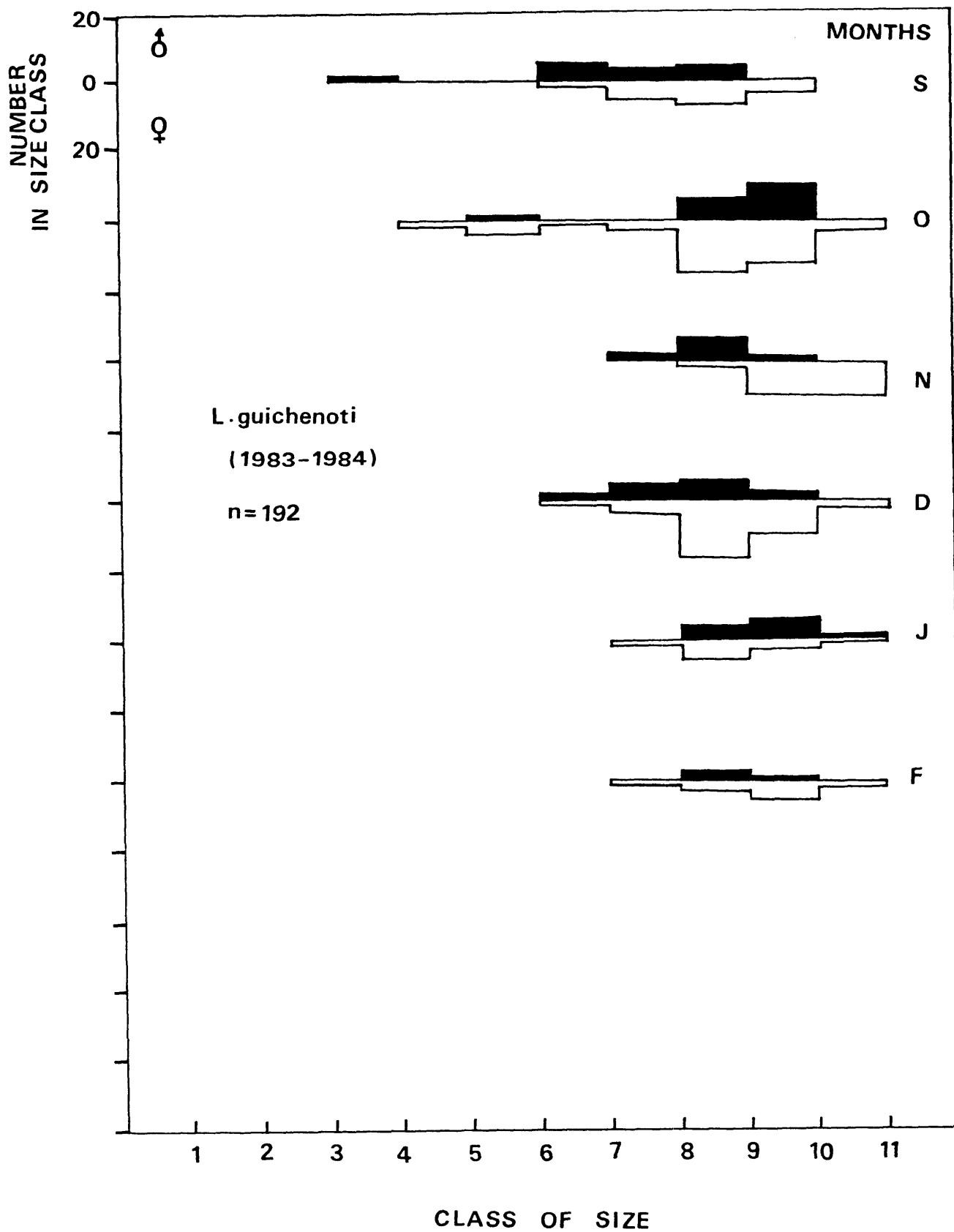
follows: 30.0-35.9, 22%; 33.0-38.9, 22%; 39.0-44.9, 33%; 42.0-47.9 mm, 23%. Females that ranged in size between 33.0 and 38.9 mm made up 14% of the total sample of females whereas those of 39.0 to 44.9 mm body size, i.e. classes 9 and 10, made up 29% and those in classes 10 and over (42.0-47.9 mm) were in the majority and comprised 57% of the total females sampled in April.

Generally, the 1981 and 1982 body size frequency distribution revealed a greater number of individuals of various body size (age) groups during spring. However, as individuals in their second growing season reached maturity in summer, there was a great overlap in body size and hence range in body size decreased (see also Fig. 41). By the time autumn set in, samples had in the majority relatively large-sized animals (classes 6 to 10) (Fig. 42).

Body size distribution for the 1983 and 1984 (Figs 41 and 43) season was similar to that of 1981 and 1982, the drier years (Fig. 42). The spring samples had a greater range of body sizes. This range decreased during summer. Summer samples had a majority of adults in which both sexes were represented (Fig. 43). The September sample included individuals ranging from 21.0-23.9 to 42.0-44.9 mm. The majority of animals in this month's sample were those ranging between 30.0-32.9 to 33.0-35.9 mm SVL for females. The largest category of females (41%) in the September sample were of older classes (8 and 9) compared with males that were of body size classes 6 and 7.

The October sample still had a large component of young animals. Animals examined ranged in size from 24.0-26.9 to 45.0-47.9 mm. For males, animals in size classes 8, 9 and 10 (size ranges 36.0-38.9 and 42.0-44.9 mm) were in the majority (52%). Among females,

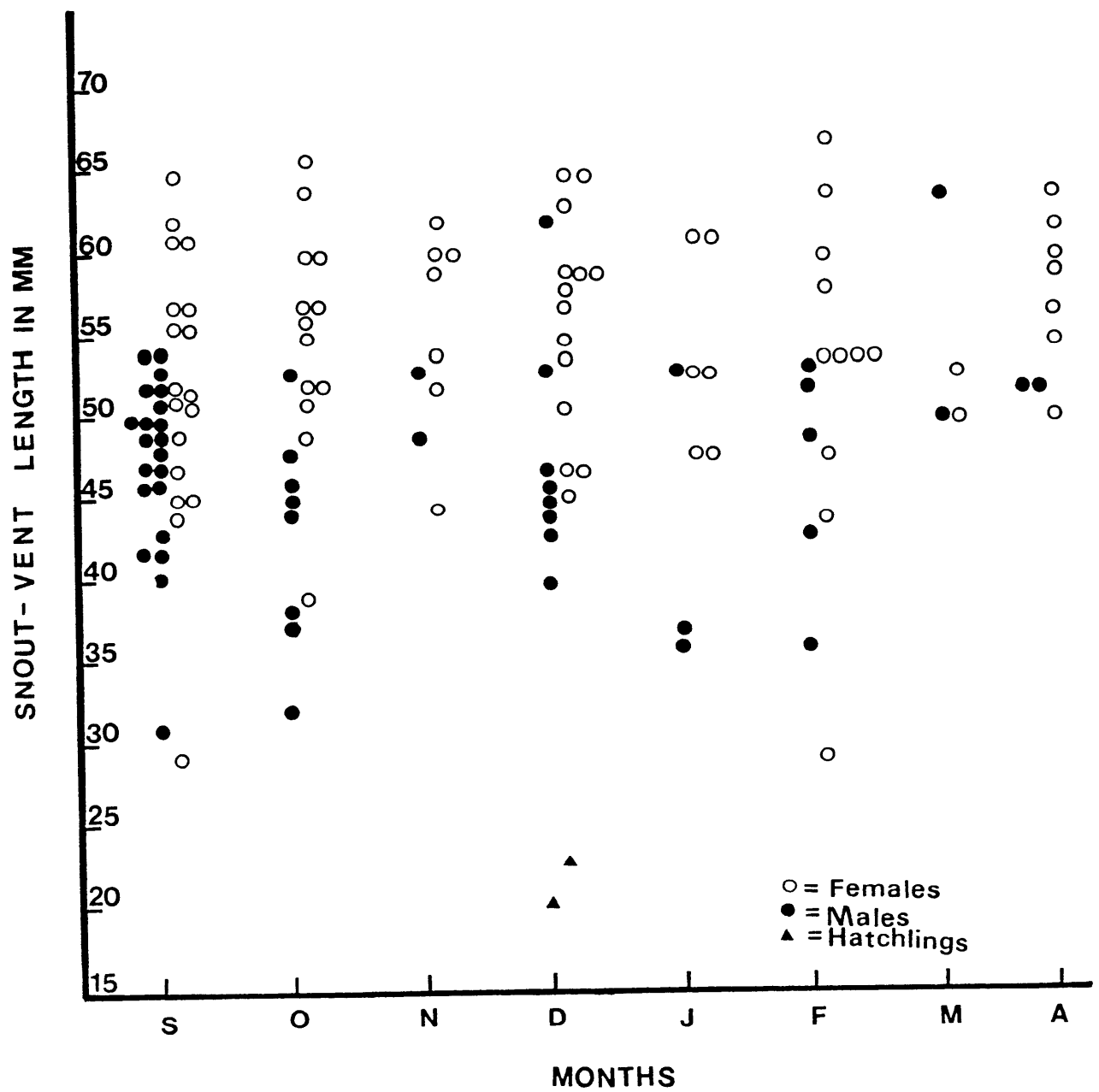
Figure 43. Body size distribution of *L. guichenoti* in the 1983 - 1984 season. No data were available for March and April, 1984.



animals of body size classes 8 and 9 (36.0-38.9 and 39.0-41.9 mm) constituted the largest class (38%). During the years 1983 and 1984, body size range decreased rather dramatically and, as early as November, only animals in body size class 7 and above were represented (see Fig. 42 for comparison). The majority of male animals in the November sample (67%) were in size classes 8 and 9 (body size ranging between 36.0-38.9 and 39.0-41.9 mm). Females whose body size ranged between 39.0-41.9 and 45.0-47.9 mm comprised 90% of the total animals examined. In December, the sample contained individuals ranging in size from 30.0-32.9 to 45.0-47.9 mm, a slightly broader range in body size than in the previous November sample. The largest number of both males (37%) and females (50%) were represented by the body size classes 8 and 9, that is, by animals whose body size lay between 36.0-38.9 and 39.0-41.9 mm (Fig. 43). In January and February, the body size range was narrowest and in favour of size classes 8 to 10. The January sample had individuals of body sizes ranging from 33.0-35.9 to 45.0-47.9 mm. Males ranging in size from 39.0-41.9 and 42.0-44.9 mm were most represented (46%) among the male animals examined in January. Among females, 56% of the animals examined were of body size range 36.0-38.9 to 39.0-41.9 mm. In February, 100% of the males were of class 8 and 9 and were of the same size range as that cited above for January females. The majority of animals in the female sample were relatively large (classes 9-10) and ranged between 39.0-41.9 and 42.0-44.9 mm.

Except for September when there was a tendency for a greater skewness towards smaller sized classes, and in November when the opposite occurred, the rest of the months had a majority of animals with body sizes ranging from 36.0-38.9 to 42.0-44.9 mm (Fig. 43).

Figure 44. Body size structure of *Hemiergis decresiensis* in the 1981-1982 season. Open circles represent individual females and closed ones males. Triangles represent hatchlings.



Body size frequency in Hemiergis decresiensis

Body size differences in *H. decresiensis* samples collected in the 1981 and 1982 season were dealt with in detail in Chapter 3. Newborn *H. decresiensis* are recruited in the population in December and have five months in which to grow before brumation (Fig. 44). Newborn grow much larger before over-wintering and unlike *L. guichenoti*, body sizes of young *H. decresiensis* in summer differ greatly from those of young that emerge in spring. Figures 44 and 45 show that females are larger than males but these size differences differ monthly and with season. However, the trend remains the same as in *L. guichenoti*, i.e. the tendency is for females to grow larger than male conspecifics (Tables 16 and 17). However, the null hypothesis that the distribution of body sizes did not differ among the sexes (Table 17 and Fig. 45) could not be rejected ($\chi^2 = 5.56$, $P > 0.05$, $df = 7$). December displayed the broadest range of body sizes among individuals. This pattern continued into September and October (Fig. 44). By November though, only sexually mature males and females were recorded (45.0 mm and larger).

Body size structure of *Hemiergis decresiensis* from the 1981-1982 season was similar to that of *Lampropholis guichenoti*. Spring samples had a greater range of animals of different body sizes whereas autumn samples were composed of adult males and females only (Fig. 46).

A September sample of male *H. decresiensis* had individuals whose body sizes ranged from 30.0 mm to 60.0 mm, whereas that of females had individuals whose body sizes ranged from 30.0 mm to 65.0 mm (Fig. 46). In the sample of males, the majority of individuals (58%) had body sizes between 45.0 and 55.0 mm. Smaller individuals (30.0 to 40.0 mm) made up 36% of the total males examined in September whereas larger males (60.0 mm and over) comprised only 6%. Among females, individuals ranging from 40.0 to 50 mm comprised 48% of the total females examined.

Larger females (55.0-65.0 mm), constituted 45% whereas smaller individuals (30.0-40.0 mm) made up only 7% of the total sample of females. In October, male sizes ranged from 30.0-55.0 mm whereas females had a broader range of body size, i.e. 35.0-70.0 mm.

There was a considerable decrease in range of body sizes among both sexes in November. This was in favour of medium-sized individuals (40.0-65.0 mm) and to the exclusion of individuals less than 40.0 mm and more than 65.0 mm (Fig. 46). Among males, 50% of the individuals examined measured between 45.0 and 50.0 mm whereas the other 50% were between 50.0 and 55.0 mm. Females of 55.0 to 65.0 mm were in the majority (63%) whereas individuals less than 55.0 mm constituted 37% of the total number of females.

The body size range for individual males and females examined in December was similar to that of the November sample. Male body size range was from 40.0 mm to 55.0 mm. Females, on the other hand, had a broad range of body sizes, from 40.0 mm to 65.0 mm. The majority (86%) of male individuals measured between 40.0 and 45.0 mm. Individuals larger than 45.0 mm accounted for only 14%. The January and February samples were taken after recruitment of newborn (in December, Fig. 15, Chapter 3), and hence had a number of small individuals represented. Among females examined in January 60% had body sizes between 50.0 and 60.0 mm. Individuals larger than 60.0 mm accounted for 20% and the other 20% was made up of animals less than 50.0 mm. In January, males of 45.0 to 50.0 mm were in the majority and these constituted 64% of the total sample of males. Thirty-six percent of the animals were of smaller body size (35.0-40.0 mm). No males over 50.0 mm were recorded. The majority (67%) of females were

Table 17. Mean monthly differences in body size of adult males and female *H. degei* in the 1981-1982 season.

MONTH	Male Snout-vent length				Female Snout-vent length				t value	P
	mean	SD	CV	N	mean	SD	CV	N		
September	45.68	10.5	22.98	21	52.19	8.9	17.05	18	2.07	< 0.05
October	43.11	6.9	16.00	10	55.51	7.1	12.79	14	4.26	< 0.001
November	55.30	5.9	10.66	11	56.40	6.2	10.99	17	0.46	ns
December	42.80	9.7	22.66	18	54.60	10.5	19.23	16	3.41	< 0.01
January	42.40	9.6	22.64	17	54.40	5.8	10.66	15	4.21	< 0.001
February	46.80	7.2	15.38	15	53.70	10.2	18.99	11	2.02	ns
March	53.10	7.1	13.37	19	57.20	9.7	16.95	10	1.29	ns
April	51.50	2.1	4.07	18	58.40	4.5	7.71	17	5.85	< 0.001

larger and measured between 60.0 mm and 65.0 mm. Animals smaller than 50.0 mm comprised 33% of the total females examined in January.

Males from the February sample ranged in size from 35.0 mm to 50.0 mm, whereas females had body sizes ranging from 35.0 mm to 70.0 mm. Among males, animals measuring between 45.0 mm and 55.0 mm constituted 84% of the total February sample. Animals less than 45.0 mm accounted for 16%. In females, animals measuring 55.0 mm and above, comprised 70% of the total animals examined whereas those below this body size constituted 30% of the total sample. Hence, large *H. decresiensis* were in the clear majority.

By March and April, samples of *H. decresiensis* had a markedly reduced body size range. Only animals between 45.0 mm and 65.0 mm were present in the samples (Fig. 46).

It is difficult to interpret variation in body size between the two sexes even when sample sizes are of similar size. Females grow much larger (Table 17) than males (Fig. 45). Hence young males are generally smaller than female counterparts of perhaps the same age. However, similar trends in body size occur in both sexes. After recruitment of newborn in December, the monthly differential growth of the young of both sexes in January and February result in a large range of body sizes. Younger (small) animals, however, are not represented in autumn samples, but are abundant in spring samples (Figs 45 and 46). The general pattern of body size structure is similar to that recorded for *L. guichenoti* from the same locality during the same years (1981 and 1982).

Figure 45. Seasonal body size variation in adult
H. decresiensis in the 1981-1982 season.
Vertical lines are ranges, horizontal lines
are means and rectangles represent standard
deviations of the mean. Numbers denote
sample size.

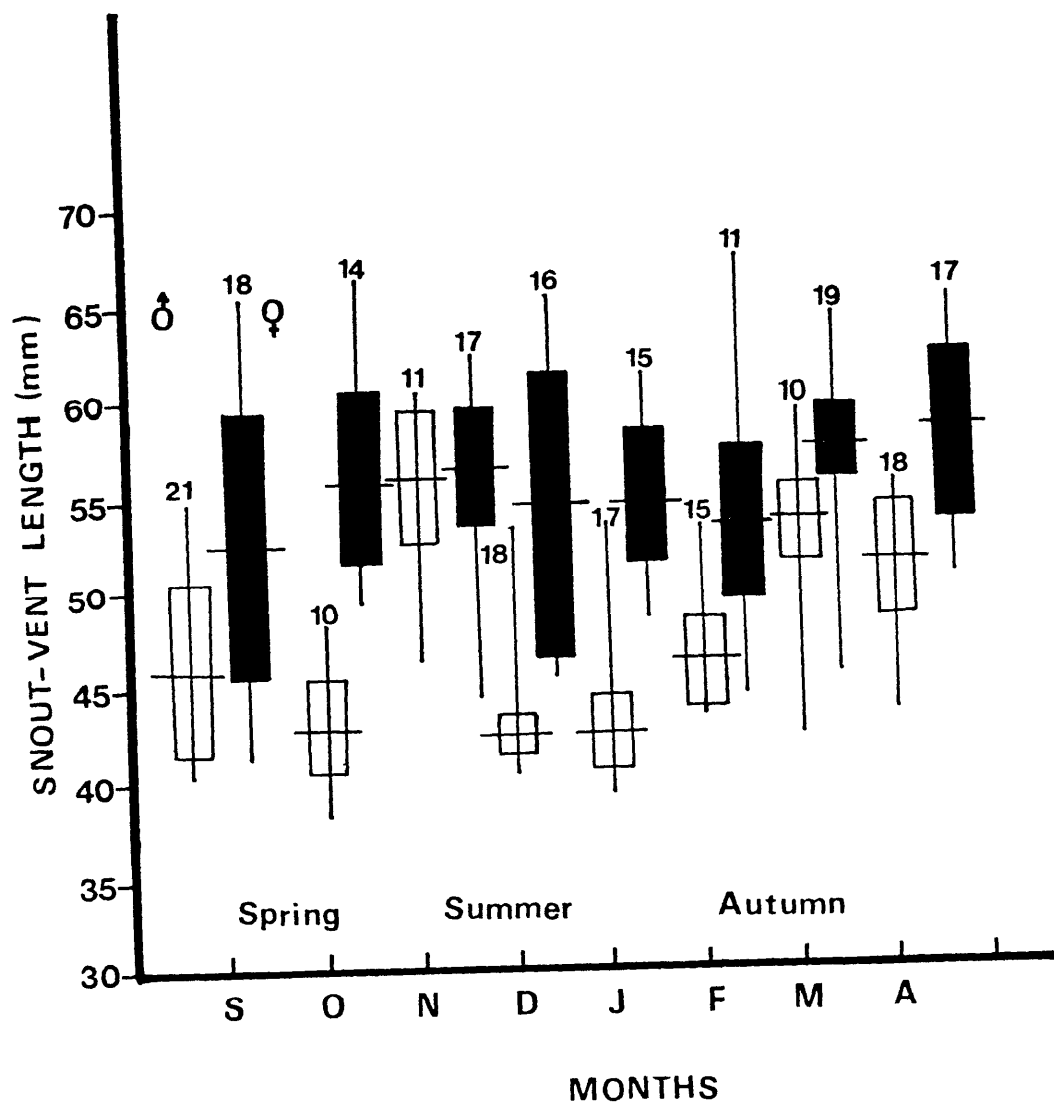
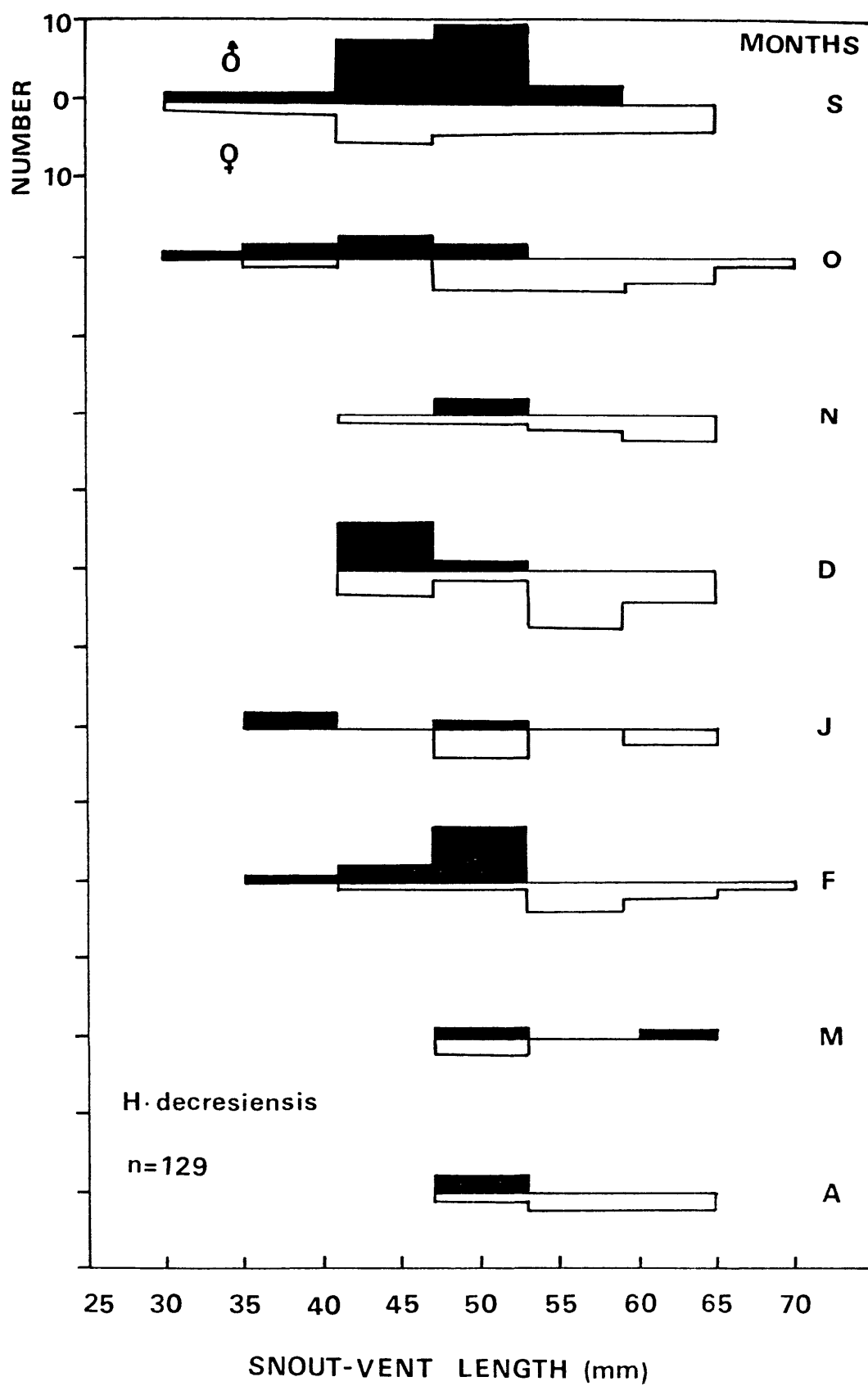


Figure 46. Body size distribution in *H. decresiensis*
from the 1981-1982 season.



DISCUSSION

Detailed studies of changes in body size structure in lizard populations have been carried out only by Fitch (1973b). The only mention of body size changes in a skink population is that of Pengilley (1972). Body size structure and stability is affected by many factors including (1) growth patterns, (2) reproductive cycles, (3) movements and behaviour of the species, and (4) longevity. All these are factors closely related to population dynamics. The last factor is also closely related to survivorship and rate of population turn-over.

Discontinuous reproduction results in discrete size classes. Fitch (1973b) provided a detailed account on how different reproductive cycles affect population size structure. Various factors affect population size structure. For example, behavioural differences between sexes, movement patterns and size of samples could affect the nature of monthly size changes in a population. But because successive samples were from the same general area, it is assumed that samples were subjected to the same bias, hence should be representative of the changes in population structure that occurred over the years.

The capture-mark-recapture programme discussed in Chapter 3 was probably not adequate to demonstrate survivorship but gave estimates of age, movements and population turn-over in *L. guichenoti*. Rate of turn-over was judged from the rate at which marked individuals disappeared from the population. This is a better estimator than survivorship which assumes that individuals that disappear from the population necessarily die. Individuals may not be recaptured again because of emigration.

Pengilley (1972) studied *Lampropholis (Leiolopisma) guichenoti* from Coree Flats, N.S.W. and found that two groups of animals were

recognizable within the population, i.e. those that were one year old (< 35.0 mm SVL) and another group over 35.0 mm SVL that included all animals two or more years old. No clear body size distribution pattern was evident, perhaps because of limited data.

The present study shows great overlap in body size with newborn and/or hatchlings predominant in December in the case of *H. decresiensis* and in February in the case of *L. guichenoti*. The population is made up of discrete groups from various years whose body sizes greatly overlap. Both skinks have a population structure in which all size (age) groups are represented at emergence in spring. When young become nearly sexually mature in their second summer, the population becomes heterogeneous with hatchlings and/or newborn, immature and adults of all sizes represented. Because both *H. decresiensis* and *L. guichenoti* reproduce only once each year (summer) both populations have well defined and separate annual cohorts.

The capture-mark-recapture study of *L. guichenoti* revealed a very low rate of recovery which showed a high rate of displacement of individuals in the population (see Chapter 3).

In both species of this study, changes in body size structure are similar throughout the year. From his study of Costa Rican lizards, Fitch (1973b) indicated that similarity in seasonal changes in population size structure among species may reflect common response to similar habits, habitats and climates. The data from the present study are consistent with his hypothesis although other mechanisms are not ruled out.

Hemiergis decresiensis grows nearly twice the maximum size attained by *Lampropholis guichenoti*.

Body size in reptiles is related to many phenomena including (1) phylogenetic position (Cope, 1896; Haldane and Huxley, 1927; Newell, 1949; Rensch, 1948 and Ricklefs, 1973), (2) aerobic capacity (Bennett, 1983), (3) capacity to change colour (Norris, 1967), (4) parasitism (Daniels and Simbotwe, 1984), (5) body temperature (Porter and Tracy, 1983), (6) feeding habits (see Chapter 2, Part 1 for details), (7) social organization (Trivers, 1972, 1976), (8) survivorship (see examples in Fox, 1978; Ferguson, Brown and de Marco, 1982; Ferguson and Fox, 1984, and (9) growth (see examples in Chapter 3, Part 2 on how changes in the weather affected body size and body weight of the population in the present study).

Information on population body size structure in reptiles lacks detail and except for Fitch (1973b), no detailed information is available for lizards. Except for brief notes in Pengilley (1972), no information on this subject exists for skinks. Clearly, more extensive studies are needed in this area and these should cover both temperate (as with the presently studied species) and tropical skinks.

CHAPTER 7

POPULATION DENSITY AND BIOMASS

CHAPTER 7

POPULATION DENSITY AND BIOMASS

INTRODUCTION

There have been many empirical and theoretical studies of the population dynamics of reptiles (Barwick, 1959; Cagle, 1946; Milstead, 1965; Heatwole and Sexton, 1966; Whitford and Creusare, 1977; Barbault, 1967, 1974e, f, 1975b, 1976; Jansen, 1976; Scott, 1976; Evans and Evans, 1980; Inger, 1980; Brooke and Houston, 1983). However, very few intensive studies have been carried out at one site over an extended time. Some studies have investigated how different climatic zones affect density and biomass in natural populations whereas others have compared biomasses and densities in analogous habitat types which are geographically isolated from each other (Jansen, 1976; Scott, 1982; Inger, 1980). Whitford and Creusere (1977) studied population dynamics and stability in Mexican desert reptiles. Similar work on insular reptile populations have been carried out at Praslin Island, Seychelles, by Evans and Evans (1980), Barrow Island, Western Australia, by Heatwole and Butler (1981) and Cousin Island, Seychelles, by Brooke and Houston (1983). Studies on Australian reptiles are few and include Fyfe (1980), Milton (1980) and Heatwole and Butler (1981).

The present study is meant to elucidate population dynamics and stability. The study will show how density and biomass relate to the weather and how these factors vary between sympatric populations of *Lampropholis guichenoti* and *Hemiergis decresiensis*.

MATERIAL AND METHODS

The study of density and biomass was carried out on a one-hectare area near Mount Duval and Sandy Creek at Newholme. The area had uniform open woodland dominated by *Eucalyptus* trees.

Population density was estimated by making transects through the habitat. The range of good visibility determined the effective width of the transects. It was 10 m in 1981-1982 (dry years) when the area was open, but only 5 m in 1983-1984 (wet years) when vegetation cover was denser. The total number of lizards observed was divided by the total surface area of the site (i.e., metres walked multiplied by the effective width of the transect) and expressed as the number of lizards per hectare. The density estimates calculated were converted to biomass estimates using data on population structure and mean body weight for the respective months (Brooke and Houston, 1983). Hatchlings and newborn were excluded because they were thought to contribute little biomass and because of their preponderance only for a brief period.

Counts were made under uniform conditions, i.e. a clear or overcast day each month and at a time when lizards were most active (see Chapter 2, Part 1). In the case of *H. decresiensis*, the microhabitats described in Chapter 1, Part 2 were disturbed, logs and litter were rolled and bark lifted and put back in position. Counts were made twice a day, i.e. between 1000 and 1300 hrs. Each count took 1 hour to complete leaving a 1-hour break for the animals to settle between counts. The smaller of the two counts was used in order to minimize the effects of counting the same animals more than once. Even so, total counts can be considered only as rough estimates.

Analytical methods

Chi-square (χ^2) tests were used to test the null hypotheses that (1) the distribution of numbers of individuals per hectare (density) per month did not vary between the years 1981-1982 and 1983 and 1984, and that (2) gram live weight per hectare (biomass) was not distributed differently between dry years (1981-1982) and wet years (1983-1984).

A Mann-Whitney two sample rank sum U test was used to test differences in annual densities and biomasses between samples.

No analysis of *H. decresiensis* data was attempted in 1983-1984 season because of insufficient records; these data are merely presented as means \pm SD.

RESULTS

Values of single species biomasses and densities are summarized in Tables 18 to 20. The relatively drier years of 1981 and 1982 were contrasted with the wetter years of 1983 and 1984. In *L. guichenoti* there was a slightly greater total number of lizards recorded annually per hectare (230) in the 1981-1982 season than during the 1983-1984 season (224), i.e. 2.6% fewer lizards were recorded in 1983-1984 (Tables 18 and 19). However, means based on total numbers of individuals per hectare were not significantly different between 1981-1982 ($\bar{x} = 28.75 \pm 4.5$, $N = 8$) and 1983-1984 ($\bar{x} = 28.0 \pm 9.44$, $N = 8$) ($U = 45.45$, $P = 0.10$). Also the null hypothesis that the distribution of numbers of individuals recorded per hectare per month did not differ between 1981-1982 and 1983-1984 (Tables 18 and 19) was not rejected, i.e. there were similar patterns of distribution ($\chi^2 = 4.36$, $P > 0.05$, $df = 7$). Annual biomass production for *L. guichenoti* showed the opposite trend to density when the drier years of 1981-1982 were compared to the wetter 1983-1984

Table 18. Density and biomass of *L. guichenoti* in 1981-82.

Area sampled was 100 x 100 m.

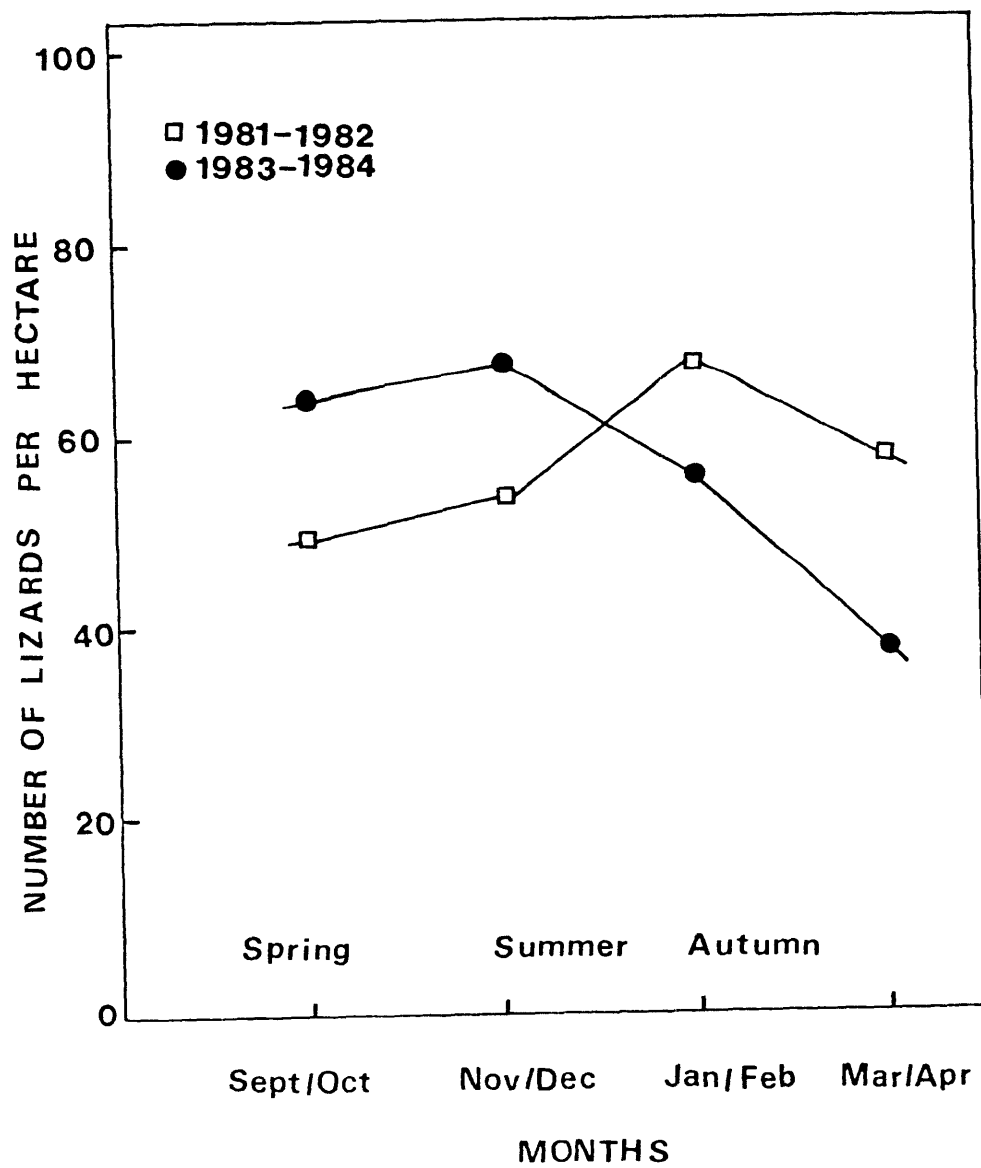
Months (1981-1982)	Individuals per hectare	Biomass in g/ hectare
September	26	26.45
October	24	24.30
November	30	29.41
December	24	25.40
January	30	32.02
February	38	37.00
March	28	27.07
April	30	31.80
TOTALS	230	233.45

Table 19. Density and biomass of *L. guichenoti* in 1983-84.

Area sampled was 100 x 100 m.

Months (1983-1984)	Individuals per hectare	Biomass in g/ hectare
September	24	30.00
October	40	39.29
November	30	37.60
December	38	40.34
January	20	19.40
February	34	35.41
March	26	28.41
April	12	13.01
TOTALS	224	243.46

Figure 47 . Monthly and seasonal variation in density of *L. guichenoti* in 1981-1982 (squares) and 1983-1984 (closed circles). See Tables 18 and 19 for sample sizes.



season. The advent of the wetter season resulted in record body weight and size values for *L. guichenoti*. Details can be found in Chapter 3. As a result of this, *L. guichenoti* had an estimated biomass of 243.46 g/ha/yr in 1983-1984 compared with 233.45 g/ha/yr in the previous years of 1981-1982. However, mean biomass for 1983-1984 (30.1 ± 9.77 (SD), $N = 8$) and that of 1981-1982 (28.8 ± 4.3 , $N = 8$) was not significantly different ($U = 39.5$, $P = 0.20$). The hypothesis that monthly biomass production in *L. guichenoti* was uniform over the years 1981-1982 and 1983-1984 was not rejected ($\chi^2 = 1.36$, $P > 0.05$, $df = 7$). This concurs with the density and biomass distribution patterns during the years 1981-1982 and 1983-1984 (Figs 47 and 48).

Density and biomass data for *H. decresiensis* are summarized in Table 20. No comparative data were available for 1983-1984. There was a mean density in 1981-1982 of 14.13 ± 11.7 per hectare and a mean biomass of 21.24 ± 19.0 .

Unlike *L. guichenoti* in which temporal changes in density and biomass were relatively slight, those of *H. decresiensis* were of greater magnitude with the largest number of individuals and the greatest biomass recorded in spring with relatively uniform moderate values in summer. By autumn the values were at their lowest (Fig. 49). This pattern is different from that of sympatric *L. guichenoti* whose peak density and biomass was in summer. The minimum values of density and biomass in *L. guichenoti* were also recorded in autumn (Figs 47 and 48).

DISCUSSION

Reproduction is basic to population dynamics and continuity of species in natural communities. Both *L. guichenoti* and *H. decresiensis* are seasonal, single-brooding species. As a consequence of this, the

Figure 48 . Monthly and seasonal variation in biomass (gram live weight/ha) of *L. guichenoti* in 1981-1982 (squares) and 1983-1984 (closed circles). See Tables 18 and 19 for sample sizes.

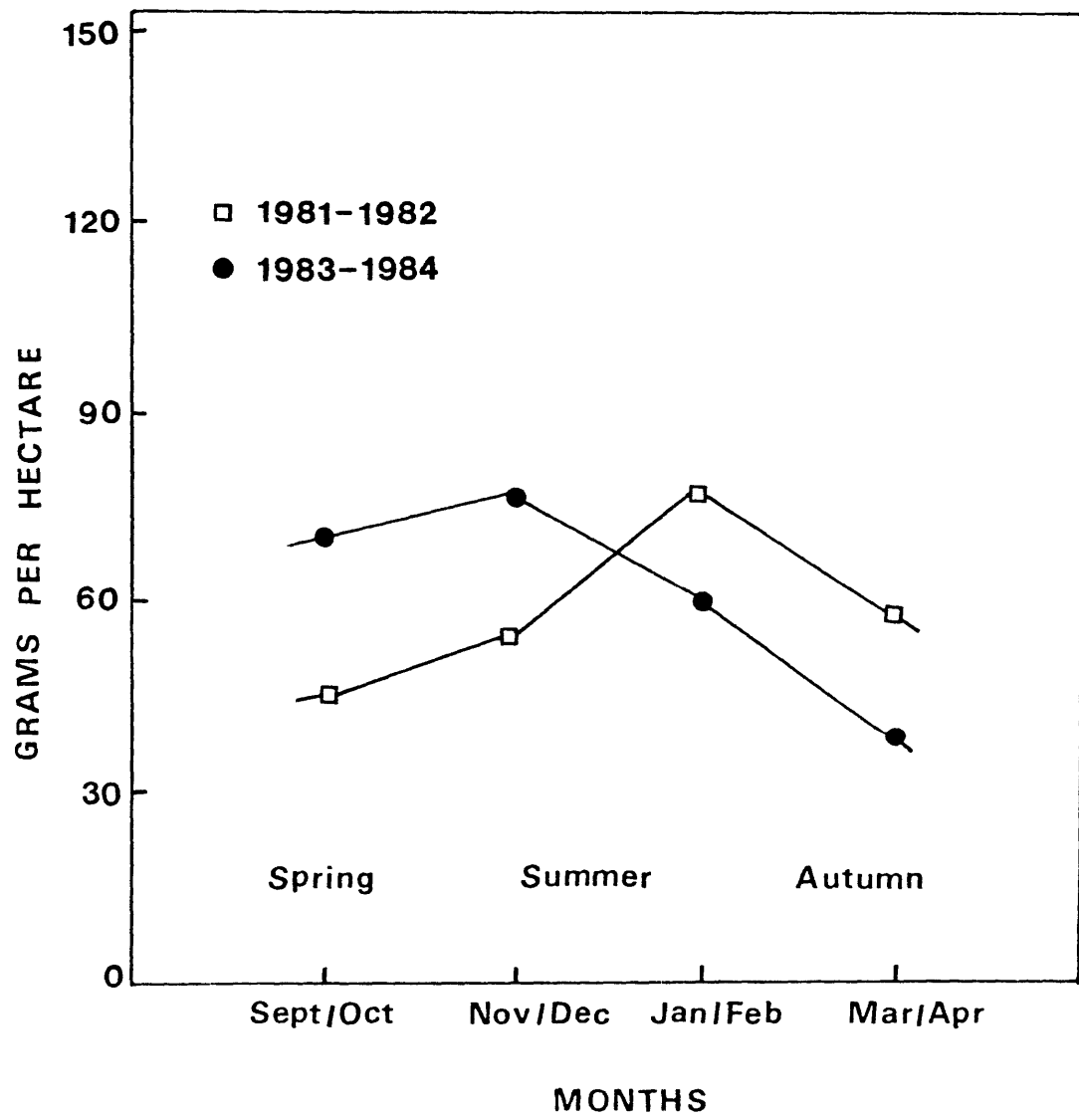
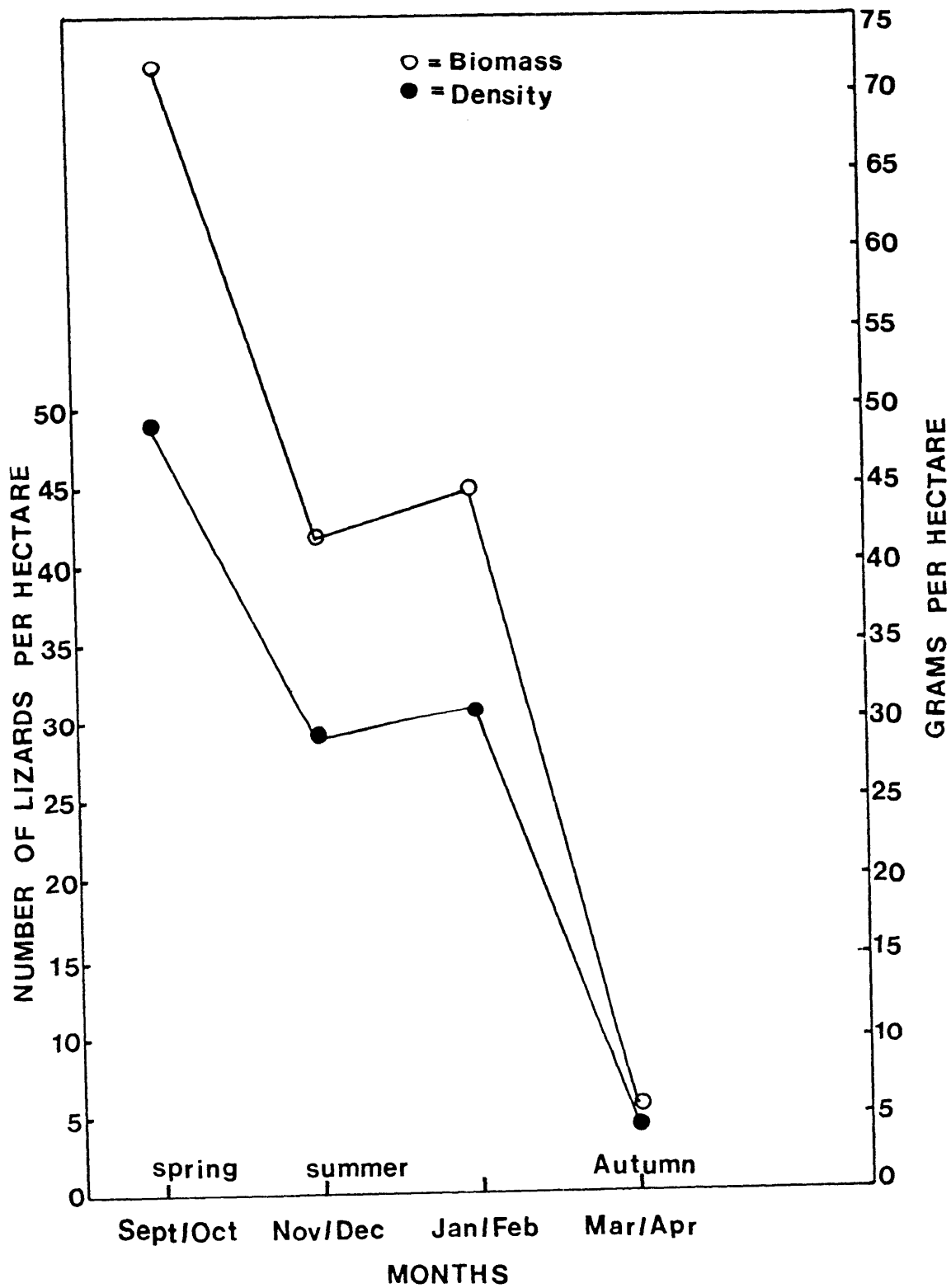


Table 20. Density and biomass of *H. decresiensis*. Area sampled was 100 x 100 m.

Months (1981-1982)	Individuals per hectare	Biomass in g/hectare
September	38	60.50
October	11	13.00
November	10	14.33
December	19	30.33
January	20	30.19
February	11	16.00
March	2	3.00
April	2	2.60
TOTALS	113	169.95

Figure 49. Monthly and seasonal variation in density (closed circles) and biomass (open circles) of *H. decresiensis* in the 1981-1982 season. See Table 20 for sample sizes.



populations at Armidale have a great infusion of different sized individuals from various overlapping generations (see Chapters 4 and 6 for details). Some workers have shown that where reproductive potential is high, in many species there is also a tendency for low survivorship. On the contrary, where species show lower fecundity, higher survivorship seems to prevail (see Duellman, 1978 for review of the ideas). Continuous successful reproduction has been claimed to be responsible for decreasing population fluctuations. Inger and Greenberg (1966b) suggested this may be one of the reasons for high species richnesses and abundances of animals, especially those inhabiting humid tropical rainforests.

Milton (1980) made crude estimates of densities of *Lampropholis guichenoti* in Toohey forest near Brisbane of approximately 90 lizards per hectare. But he did not say whether this was a monthly estimate and/or whether it involved all age/size groups. Fyfe (1980) studied lizards in burnt and unburnt sites in central Australia. He found that relative densities of lizards in unburnt sites was 1 to 21 lizards, whereas a significantly lower number was recorded in burnt areas, i.e. 1 to 12 lizards only. This supports the suggestion that population dynamics of reptiles is greatly affected by disturbances like fire. Fire may act on the population in two ways; by killing eggs, young and adult lizards, or by destruction of grasses, litter, fallen timber and other microhabitats preferred by floor-dwelling lizards. Removal of woodland floor cover in Newholme would expose the skinks there to their bird, snake and mammalian predators. The role of predators and fire in the regulation of reptile abundances is discussed by Jansen (1976) who proposed that competition among reptiles and non-reptilian competitors may also be a significant depressant of reptile densities, especially so in African savannas (but see Kruegen, 1979).

General comparisons have been made concerning reptile abundances in relation to altitude by Inger (1980). He found that by comparing lizards and frogs in lowland forests of southeastern Asia and central America, there were between-communities and between-years differences in densities among similar populations, much as in the present study of *L. guichenoti* and *H. decresiensis*. These differences, however, may have been mere reflections of a temporary seasonal phenomenon (Inger, 1980).

When between-community or ecotypic relations are considered, *H. decresiensis* is found to be occupying more mesic microhabitats than does *L. guichenoti* (Daniels and Simbotwe, 1984). The floods of 1983-84 in Newholme nearly wiped out the whole *H. decresiensis* population (Chapter 6). *Lampropholis guichenoti* seemed not to be affected as much. The difference may be in reproductive potential. When newborn of *H. decresiensis* start to appear in December, they are not as commonly encountered as are hatchlings of *L. guichenoti*. Because adult *H. decresiensis* rarely venture far from cover and move much slower than *L. guichenoti*, many are likely to drown in the event of flash floods, and few could make it to high ground. Some *L. guichenoti* were found floating on logs when flood water had covered the whole study area. Floods generally resulted in spatial displacement of individuals and probably caused death by drowning. However, even among individuals that were found dead, cause of death could not be ascertained.

Some workers have looked at the effects climate has on reptile densities. One basic assumption of these studies is that differences in herpetofaunal densities is causally related to differences in climatic parameters, especially precipitation. The major variables in rainfall include number of dry months and total precipitation. Some

studies have shown that areas with the greatest herpetofaunal densities also have a more continuously wet climate (Scott, 1976). The advent of the rainy season induces vegetative growth which provides food for primary consumers upon which secondary consumers like lizards depend. Whitford and Creusere (1977) found that lizard densities varied greatly with rainfall-induced changes in productivity, i.e. relative abundance of primary consumers (arthropods). Increased density during the wet years of 1983-1984 among *L. guichenoti* populations may have been a result of this. Other positive indicators during the same period for *L. guichenoti* were increases in body size, body weight, and clutch size (see Chapters 3 and 4).

Lizard densities have been studied on islands as a means of answering the following questions: (1) What is the effect of competitive interference on island communities with respect to animal abundances? (2) Do islands exhibit greater insect productivity in relation to equivalent habitats on the mainland and how does this affect reptile densities? (3) How does reduced predation intensity on islands or a combination of all these factors influence animal abundances (see also Case, 1975). Heatwole and Butler (1981) recently studied the reptile fauna of xeric *Triodia* habitat from Barrow Island, Western Australia. The twelve species of lizards studied had a collective density of 324 individuals per hectare. The three most abundant species had densities of slightly over 50 individuals per hectare each. These values were not particularly different from those of the present study. But some island lizards can be very abundant and such is the case for a skink, *Mabuya sechellensis* with records of 1,393 individuals per hectare (Brooke and Houston, 1983). But this same skink on Praslin Island showed the following variations in densities: 221 individuals per hectare in coastal vegetation transects,

320 in intermediate forest, 150 in lowland forest and 94 in eroded land (Evans and Evans, 1980). *Mabuya wrightii* was sympatric with *M. sechellensis* (Brooke and Houston, 1983), but the former had densities of 320 individuals per hectare only. Such differences between species densities in the same locality is widespread and was true of the present study. One important feature of this study is the fact that individuals belonging to *H. decresiensis* were at all times rare whereas the sympatric population of *L. guichenoti* occurred in greater density. The inequitable numbers of individuals between *L. guichenoti* and *H. decresiensis* is something common to many lizard communities (Heatwole and Sexton, 1966; Scott, 1976).

Apart from tropical rainforests and islands, work on lizard densities has been carried out in savannas in South America and Africa (Jansen, 1976). Barbault (1967, 1973, 1974a, 1974b, 1975, 1976) studied densities and biomasses in north African savanna herpetological communities and provided density values ranging from 1.4 to 86.7 lizards per hectare. The interesting part of his results is the comparison of open savanna and wooded savanna, and that a prolonged dry season produced fluctuations in densities comparable to those produced by burning (Fyfe, 1980), severe winters and floods. The last two factors, together with light sheep and cattle grazing, seem to be causal factors of depression of lizard density in the Newholme populations of *L. guichenoti* and *H. decresiensis*. Figures on lizard densities in the present study fall in the range of those recorded by Barbault but higher values are given elsewhere, e.g. Barwick (1959) recorded 365 individuals per hectare for *Leiolopisma zelandica*; Milstead (1965) had records of up to 185 per hectare for *Cnemidophorus tigris* in Texas; Heatwole and Sexton (1966) recorded higher values of 1,115 per hectare for *Anolis limifrons* from Panama; Jenssen (1970)

recorded 570 *Anolis nebulosus* from Mexico; Turner and Gist (1970) recorded 325 individuals per hectare of *Anolis gundlachi* in Puerto Rican montane rainforest; Turner *et al.* (1976) recorded 239 individuals per hectare for *Uta stansburiana* in Nevada.

Extremely high densities have been reported by some workers, e.g. Cagle (1946) recorded 3,950 individuals per hectare for a Pacific island gecko and Ruibal and Philibosian (1974) recorded 5,600 individuals per hectare for *Anolis acutus* on the island of St. Croix (see Heatwole and Butler, 1981, for a complete appraisal).

Even though data on population biomass of skinks is increasing rapidly, no detailed review tests this topic. Annual biomass production in *L. guichenoti* was greater in the wetter years of 1983-1984 than the relatively drier years of 1981-1982. However, estimation of annual biomass production is difficult because of a lack of knowledge of annual mortality losses (Iverson, 1982). Information on mortality in natural populations is difficult to obtain. Hence, estimates of biomass in this study were based on density estimates following the methods of Evans and Evans (1980).

Studies of reptilian and amphibian biomasses show similar trends to those of density. Biomass reaches incredible levels on islands.

Barbault (1967, 1975b) provided records ranging from 49 g to 297 g biomass live weight per hectare for reptiles of the Ivory Coast savanna. Elsewhere high biomasses have also been recorded. For example, Jenssen (1970) recorded 770 g live weight per hectare for *Anolis nebulosus* from Mexico. Busack (1975) found the biomass of *Acanthodactylus* from the pre-Saharan steppe of Tunisia to be 2,154 g live weight per hectare, whereas Evans and Evans (1980) recorded biomass estimates of 2,440 g per hectare for *Phelsuma sundbergi* from Praslin Island, Seychelles. Incredibly high values have been recorded

for *Mabuya wrightii* from (up to 17,700 g per hectare) and even higher ones (up to 21,700 g) for *Mabuya sechellensis* from the same island (Brooke and Houston, 1983). Biomass of both skinks was positively correlated with environmental productivity, i.e. with the number of noddy nests. Ruibal and Philibosian (1974) recorded 23,000 g live weight per hectare for *Anolis acutus*.

The only biomass estimates of Australian reptiles are those from Barrow Island, Western Australia, studied recently by Heatwole and Butler (1981). Biomass was established to be about 3,110 g per hectare live weight and 779 g per hectare dry weight respectively. Clearly, there is a need for studies of density and biomass among Australian reptiles, especially skinks.

Biomass estimates are available for hundreds of species of African mammals and now estimates of biomasses are available for a large number of turtles (Iverson, 1982). Equivalent information on lizards is lacking, especially for skinks. Such information would be useful for assessing energetics and for solving special problems that face conservationists, such as rate of recovery of reptile populations in their natural environments (see also Iverson, 1982).

CHAPTER 8

SUMMARY AND CONCLUSIONS

CHAPTER 8

SUMMARY AND CONCLUSIONS

The present work deals with the ecology and demography of sympatric populations of *Lampropholis guichenoti* and *Hemiergis decresiensis* at Newholme, Armidale. The topic is dealt with in detail in seven chapters. In each chapter, the objectives of the work, field and laboratory techniques, methods of data analysis and results are presented in detail. The relevance of each topic to theory and areas in which more work is needed are pointed out in each chapter.

The aims of this chapter are (1) to point out the findings of major importance and make brief comments on them and (2) to summarize the most important discoveries.

SUMMARY AND CONCLUDING REMARKS

PART 1, CHAPTER 1. ECOLOGY AND DEMOGRAPHY AMONG LIZARDS OF THE
FAMILY SCINCIDAE: AN OVERVIEW.

1. Out of 56 species of skinks reported upon in the literature 23 (41.1%) were of temperate distribution and 33 (58.9%) were tropical.
2. Minimum size at maturity ranged from 26 mm to 107 mm SVL.
3. Mean size at maturity ranged from 36 mm to 136 mm SVL.
4. Age at first reproduction was as early as 6 months in small skinks to as late as 36 months in larger ones.
5. Of the 25 species that had complete data on clutches per season, 12 species were single-brooded whereas 13 were multiple-brooded.

6. Of the aforesaid 25 species, 10 were temperate and of these, 9 species produced single clutches per season whereas only 1 produced multiple clutches. The remaining 15 species were tropical and of these, 3 were single-brooded and 12 were multiple-brooded.
7. Data on mode of reproduction was available for all 56 species analyzed and of these 38 practiced oviparity, 17 were viviparous and 1 was ovoviviparous.
8. Of the 23 temperate species, 8 were viviparous whereas 15 were oviparous.
9. Of the 33 tropical species, 8 practiced viviparity, 24 were oviparous and 1 was ovoviviparous.
10. Mean clutch size for all skinks ranged from 1 to 13 eggs and out of 49 temperate and tropical clutches analyzed, mean clutches of 2 eggs were by far the most prevalent. It was generally concluded that 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.

PART 2, CHAPTER 1. ENVIRONMENT.

Scarcity of rainfall in the years 1981-1982 apparently caused biological problems for *Lampropholis guichenoti* and *Hemiergis decresiensis*.

11. Little rainfall in the 1981-1982 season resulted in stunted and light animals of both species; they were heavily infested with acanthocephalan cystacanths.

12. The wetter 1983-1984 season produced larger and heavier *L. guichenoti* individuals. Clutch size also increased during this season. However, flash floods nearly wiped out the whole population of *H. decresiensis*.

PART 1, CHAPTER 2. TEMPORAL, THERMAL AND FOOD NICHE.

13. Both the heliothermic, diurnal lizard *L. guichenoti* and a presumed "noctinodiurnal", thignothermic lizard, *Hemiergis decresiensis* were found to have similar daily activity patterns.
14. Most activity was restricted to 1000 to 1300 hours, and most activity started to decrease between 1400 and 1500 hours with no activity recorded after 1800 hours.
15. Adult *L. guichenoti* had a bimodal pattern of activity with peaks occurring early in the day when its microhabitats were warming up and again later when the environment was cooling down.
16. *Hemiergis decresiensis* was found to be active an hour later in the day than *L. guichenoti*.
17. There was a weak relationship between cloacal temperature and air temperature in *L. guichenoti*, but by contrast there was a strong, statistically significant relationship between cloacal temperature and substrate temperature.
18. Body temperature of *L. guichenoti* was normally 18°C at morning emmergence, but quickly rose to between 20° and 31°C during the day.
19. The time niche breadth of *L. guichenoti* was 0.406 whereas that of *H. decresiensis* was 0.337.

20. The activity time niche overlap between the two species (Ojk) was 0.908.
21. Beetles, spiders, lepidopteran larvae, flies and ants were among the largest number of arthropods eaten by *L. guichenoti* during the summer months.
22. Termites, ants, lepidopteran larvae and beetles comprised a significant part of the diet of *H. decresiensis*.
23. A null hypothesis that there were no differences in the frequency with which the two species ate different food items was retained. This was also supported by a large food niche overlap value (Ojk = 0.749).
24. Both species were found to eat primarily hymenopterans, isopterans, coleopterans and lepidopterans.
25. Even though present in the study area, centipedes, crickets, leaf-hoppers, millipedes, scorpions and wolf spiders were not eaten. The reason is not known, but could include crypsis, unpalatability and illusiveness.
26. Head size of *L. guichenoti* showed a highly significant relationship with mean prey size, suggesting that large animals tended to eat larger prey than small animals.
27. The food niche breadth was 0.445 for *L. guichenoti* and 0.251 for *H. decresiensis*.

It was concluded that any similarities and differences in diet between the two species could be accounted for largely by the nature of foraging and by microhabitat overlap. 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.

Overlap in time of activity is very high among the two species, confirming the experimental results of Firth (1968). The restricted activity period of *H. decresiensis* in comparison with that of *L. guichenoti* may be a result of the damp microhabitats of the former, which may warm much more slowly than the drier, more open microhabitats of the latter species.

Time of day was found to influence air and substrate temperatures.

PART 2, CHAPTER 2. HABITAT USE.

28. Both species utilized similar microhabitats of fallen wood, grasses, litter, bark and rock piles.
29. *Hemiergis decresiensis*, unlike *L. guichenoti*, was active under cover such as fallen timber and ground litter during the day.
30. As a result of die-back, most trees had bark heaped at the base and these areas were popular day time and night time retreats for both species of lizards.
31. These lizards were also found to shelter communally either as single-species or in mixed-species aggregations of *H. decresiensis*, *L. delicata* and *L. guichenoti*.
32. Two likely predators with activity times and microhabitats that overlapped with the skinks in the study area, were *Pseudechis porphyriacus* and *Pseudonaja textilis*. The former was observed feeding on *Amphibolurus muricatus* in the study area.
33. With a structural niche diversity of 0.624, *L. guichenoti* uses a greater variety of substrates than *H. decresiensis* which had a niche diversity of only 0.492.

34. Structural niche overlap was 0.481 and was lower than for either the time or food niches.
35. A chi-square test on microhabitat data revealed that the two species selected microhabitats with different frequencies.
36. Of the 66 *L. guichenoti* subadults and adults marked and released in the summers of 1982 and 1983 only 8 were recovered and 5 of them recaptured twice after the initial capture and marking. Fifty-eight animals were never recaptured which showed a low rate of recovery and a high population turn-over rate.
37. Recaptured individuals were used in studies of movement patterns. Among recaptured individuals was included a hatchling which had moved at least 10 metres since marking. Adults were found to have moved a minimum of 37 metres.

It was concluded that even though the two skinks tended to occupy similar microhabitats, *H. decresiensis* was more limited in its range of microhabitats than the sympatric *L. guichenoti*. This could be attributed to *H. decresiensis*' morphology (weak limbs which result in slow movement) and thermal behaviour (mesic adapted) which confined the animal to activity under cover. Both species take advantage of bark heaped at the bases of trees and use it for day time and night time retreats. Individuals of the same and different species display communal sheltering and use similar substrates. Such common use of similar microhabitats could be responsible for similarity in food and may explain why cystacanths of the helminths *S. rotundocapitatus* use multiple transport hosts in Newholme (see Appendix 3).

PART 1, CHAPTER 3. GROWTH

38. Hatchlings of *L. guichenoti* first appear in February and are active and grow for four months before their first winter brumation.
39. By the time hatchlings enter the winter inactivity period, their umbilical scars have healed.
40. Newborn of *H. decresiensis* appear in December and grow about 5 months before their first winter brumation.
41. Growth is minimal over winter. Overlapping generations result in a wide range of body sizes within the population.
42. In both species, subadults grow relatively fast with growth being reduced considerably when individuals attain sexual maturity and slowing down even more among older individuals.
43. Hatchlings of *L. guichenoti* marked in summer showed a growth rate of 0.03 mm per day whereas older individuals marked at the same time had growth rates ranging from 0.04 to 0.01 mm increase in SVL per day.

PART 2, CHAPTER 2. BODY SIZE, SHAPE AND TAIL LOSS

44. Males of *L. guichenoti* and *H. decresiensis* have maximum snout-vent lengths of 43 mm and 64 mm respectively. The corresponding values for females were 46 mm and 67 mm respectively.
45. *Hemiergis decresiensis* reaches sexual maturity at about the maximum size attained by *L. guichenoti*.

46. In both species, females are larger than males, but sexual dimorphism in size is more pronounced in *H. decresiensis* than in *L. guichenoti*.
47. Females tended to have longer tails than males in both species.
48. There was a tendency for tail loss frequency to increase among larger (hence older) *L. guichenoti* and *H. decresiensis*.
49. There was a shift towards increased growth in body size (SVL) and body weight in *L. guichenoti* during the wetter years of 1983 and 1984.
50. *Hemiergis decresiensis* is more streamlined than *L. guichenoti*. The smooth body scales and streamlined body is advantageous to animals moving through litter and small holes in logs and rock crevices.
51. An analysis of covariance (ANCOVA) showed that body size (SVL) was strongly correlated with head measurements.

CHAPTER 4. FEMALE REPRODUCTIVE CYCLE

52. Timing of reproduction in both species depends on the length of the over-wintering period which also depends on the prevailing weather, temperature and rainfall.
53. Reproductive state in both species is characterized by three stages of ovarian development as determined by ovarian follicular colour. The latest stage of ovarian growth and oviductal eggs occurred between September and February in *L. guichenoti* and up to March in *H. decresiensis*.

54. Hatching of eggs occurs in February to early March in *L. guichenoti* and most copulations were observed from October to November, a month or two before egg deposition.
55. Both species lack strict synchronization of reproductive cycles among females; some females breed early whereas others do so later.
56. Multiple clutches do not occur in *L. guichenoti*.
57. Incubation time in the wild at soil temperatures of 21^o-25^oC is estimated at 56 to 74 days in *L. guichenoti* at Newholme.
58. From April onwards of the 1981-1982 season, female *L. guichenoti* were found to have *corpora atretica* (degenerating ova); this occurred as early as February in the wetter years of 1983 and 1984.
59. There was a yearly difference in number of oviductal eggs in *L. guichenoti*. Three eggs was the largest number in the drier years of 1981 and 1982 whereas 4 eggs was recorded in the wetter years of 1983 and 1984.
60. Mean ratio of wet clutch weight to total weight (body + clutch) was 0.138 for female *L. guichenoti* with a mean SVL of 42.6 mm.
61. In *L. guichenoti*, a clutch of 2 eggs was most frequent in the 1981-1982 season whereas in the wet years of 1983 and 1984 a clutch of 3 eggs was most frequent.
62. The number of eggs in a clutch seemed to increase linearly with increasing body size (SVL) in *L. guichenoti*.
63. Females reach sexual maturity at the same age as males in *L. guichenoti*.

64. The peak of gravidity coincided with an increase in both rainfall and temperature but this relationship was not statistically significant.
65. Fat bodies are greatly reduced by the end of summer and start to build up in autumn prior to the winter inactivity period.
66. There was a monthly deviation in apparent sex ratio from 1:1 and in most cases it was in favour of females. This was attributed to differences in behaviour between the two sexes.
67. The right ovary in both species is slightly more anterior than the left one. This morphological feature seems to be widespread among skinks.
68. Timing of reproduction in *H. decresiensis* is similar to that of *L. guichenoti* and depends on the length of brumation and prevailing weather.
69. Reproductive states described for *L. guichenoti* were similar to those seen in *H. decresiensis*.
70. Immediately after the winter inactivity period, ova mature in the ovaries. This occurs rather more quickly in *H. decresiensis* than in *L. guichenoti*. Ovulation occurs as early as October in the former.
71. Newborn *H. decresiensis* appear in December, a month earlier than hatchlings of *L. guichenoti*; no multiple births occur in a single season.
72. Based on information from time between ovulation and first appearance of newborn, gestation in *H. decresiensis* is rapid and lasts slightly over 30 days.

73. The most frequent brood size of *H. decresiensis* was 2 embryos. No data were available in the 1983-1984 season to enable comparisons to be made between years.
74. Age at maturity is attained in *H. decresiensis* at approximately 12 months.
75. The secondary sex ratio was slightly skewed in favour of females in *H. decresiensis* but this difference was not significantly different from 1:1.

CHAPTER 5. MALE REPRODUCTIVE CYCLE

76. The male cycle of *H. decresiensis* and *L. guichenoti* is similar in that testes are limp and small at emergence in spring and reach their maximum at the time when females are at their reproductive peak in summer.
77. Generally, in *L. guichenoti*, testes are at their minimum in spring shortly after emergence from brumation and at this time semeniferous tubules are small and appear evacuated. Testes reach their maximum size in the summer months of December to February.
78. The smallest mature male of *L. guichenoti* was 32.8 mm SVL.
79. The right testis of both species is more anterior than the left one.
80. Testis size increased with increase in body size in both species.
81. The male cycle of *L. guichenoti* coincided with an increase in amount of rainfall and rise in temperature and with the peak of female reproductive activity, but correlations between these parameters were weak and not significant.

82. The male cycle of *H. decresiensis* coincided with an increase in rainfall and rise in temperature.
83. No obvious external features distinguish the two sexes of either species. Autopsy records showed that except for 1981-1982 season in *L. guichenoti* females of both species are larger than their male conspecifics.

CHAPTER 6. SIZE STRUCTURE OF THE POPULATION

84. In *L. guichenoti*, there is a broad range in body sizes during the spring months of September to November, which narrows considerably during summer (December and January) and is narrowest in autumn (February to April).
85. Because reproduction is discontinuous in *L. guichenoti*, the time that hatchlings are active is limited (4 months) and because growth is reduced over winter, in the spring there are individuals of different sizes belonging to different, overlapping generations.
86. In *L. guichenoti* there is monthly and seasonal variation in average body size. Body size distribution was similar in 1981-1982 and 1983-1984.
87. In *H. decresiensis*, body sizes of individuals from various overlapping generations are more discrete, because newborn of this species have 5 months in which to grow before brumation.
88. December (when the newborn appear) is the time when the broadest range of body sizes occur in *H. decresiensis*. This pattern is altered in autumn when there are mainly sexually mature individuals in the population.

CHAPTER 7. DENSITY AND BIOMASS OF THE POPULATION

89. There was nearly the same number of individuals of *L. guichenoti* recorded in the dry 1981-1982 season as in the wetter 1983-1984 season (about 224-230 per hectare).
90. The advent of wetter conditions (1984-1984) resulted in record body weight for *L. guichenoti*.
91. *Lampropholis guichenoti* had an estimated standing crop biomass of 243.42 g/ha/yr in 1983-1984 and 233.45 g/ha/yr in 1981-1982.
92. In *Hemiergis decresiensis*, the greatest densities and biomass were recorded in spring, with relatively uniform moderate values in summer. By autumn these values were at their lowest. Estimated biomass in 1981-1982 was 169.95 g/ha/yr. Mean annual density was 113 individuals/ha.