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**Reproduction and growth of the black shore skink,
Leiolopisma suteri (Lacertilia: Scincidae),
in north-eastern New Zealand**

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Reproduction and growth of a boulder beach population of the nocturnal skink *Leiolopisma suteri* on Motutapu Island were studied for 19 months. Epididymes contain sperm from April to November, and copulation probably occurs in October or November (spring). Ovulation occurs in late October or early November, and three or four (mean, 3.7) eggs are laid in late December. Incubation takes 3 months. Total development time from ovulation to hatching is 5 months, one of the longest development periods recorded for Scincidae. Growth to sexual maturity is slow, most females depositing their first clutch 33 months after hatching; males mature at 29 months.

INTRODUCTION

Leiolopisma suteri (Boulenger) is restricted to the north-east of the North Island of New Zealand, mainly on offshore islands, where it inhabits boulder beaches and rock platforms. It is nocturnal, and is the only known oviparous lizard indigenous to New Zealand (Whitaker 1968a), although oviparity is the most common form of scincid reproduction (Greer 1968a).

Several workers have found a predominance of viviparous or ovoviviparous reptiles at high altitudes (Weekes 1933, Greer 1968b, Fitch 1970), and it has been suggested that this may also hold for areas in higher latitudes, such as New Zealand (Robb 1973). Pursuing this postulation, it might be expected that an oviparous species within the New Zealand lizard fauna would tend to retain its eggs within the oviduct to reduce incubation time, a practice common to many members of the skink family (Tinkle 1967). I have investigated this possibility in the course of an M.Sc. thesis study of the life history of *L. suteri*, for comparison with Barwick's (1959) study of the viviparous *L. zelandicum*.

The ecology of a boulder beach population of *L. suteri*, and details of the study area, are discussed elsewhere (Townes 1975).

METHODS

Data on growth rates were obtained by capture/recapture and by comparing monthly size frequency distributions from July 1971 to October 1972. Each month at least 30 individuals were measured from snout to vent (mm SV).

Maturity was determined for living animals from loss of the grey coloration of the under-surface of juveniles, the presence of swollen hemipenes in males, and the presence of oviduct eggs in females.

The reproductive cycle was elucidated by dissecting 127 individuals, of which 61 were obtained from Cable Bay over a 19-month period (Table 1). The balance came from most of the other areas in which *L. suteri* has been recorded, from the Poor Knights Islands to

		Adults	Juveniles	
♂♂	Cable Bay	22	1	23
	Elsewhere	28	3	31
♀♀	Cable Bay	35	3	38
	Elsewhere	31	4	35
		116	11	127

TABLE 1—Specimens of *Leiolopisma suteri* used for determination of the reproductive cycle. The sex ratio of adults from Cable Bay did not differ significantly from unity ($P > 0.05$; χ^2 test)

the Mercury group. Generally, only adults were collected for information on the reproductive cycle. The smallest adult male (i.e., with testes of similar size to those of larger specimens in the same sample) was 68 mm SV. Immature males had smaller testes than mature males, with thin epididymes, and immature females contained very small ovaries and small, transparent oviducts. The seasonal variation in the size of testes and ovaries was determined by *in situ* measurement of testis length and follicle or egg diameter. Both testes were measured in males, and the four largest ovarian follicles or all the oviduct eggs were measured in females. Further data were obtained from thin sections of testes and epididymes taken from selected individuals, usually one per month. These histological samples were embedded in wax, sectioned at 10 μ m, and stained using Berg's method for spermatozoa (Luna 1968).

SEXUAL DIMORPHISM

Members of the genus *Leiolopisma* typically show little sexual dimorphism, and are often very difficult to sex without dissection (Barwick 1959). This applies to *L. suteri*, although some sexual dimorphism is apparent in the breeding season. Adult males emerge from hibernation in July or August with enlarged hemipenis sacs, which cause a swelling about the cloaca.

From August to November, females become bright orange ventrally, from the fore limbs to the cloaca. This region assumes a cream-yellow colour throughout the rest of the year, except during November, when in gravid females it often becomes pink, the eggs being visible as white marks against the skin. At this time the greatly distended abdomen of the female makes sexing relatively simple. Males are often grey-green or cream-yellow over the venter during the breeding season, with orange colouring around the hemipenis sacs.

The colour of the undersurface of adults differs from that of juveniles, which is grey speckled with black. The speckling disappears as the skinks become sexually mature. This colour variation was not consistent for all populations sampled, however. Some adult individuals of 85 mm SV from Cuvier Island and the Mokohinau group had retained the grey 'juvenile' colour, as had a few individuals at Cable Bay captured away from the main breeding population. The reason for this variation is not known.

REPRODUCTIVE CYCLES

MALE CYCLE

The testes lie posterodorsally in the body cavity, the right testis lying slightly forward of the left testis. The epididymis is elongate, extending back to the kidney, where it straightens to form the vas deferens, which leads to a urinogenital papilla in the cloaca. A yellow, elongate adrenal body lies dorsal to each testis.

The testes reached maximum size in March (Fig. 1), when the seminiferous tubules were visibly swollen; however, the epididymes, though coiled, were not obviously turgid (Fig. 2a).

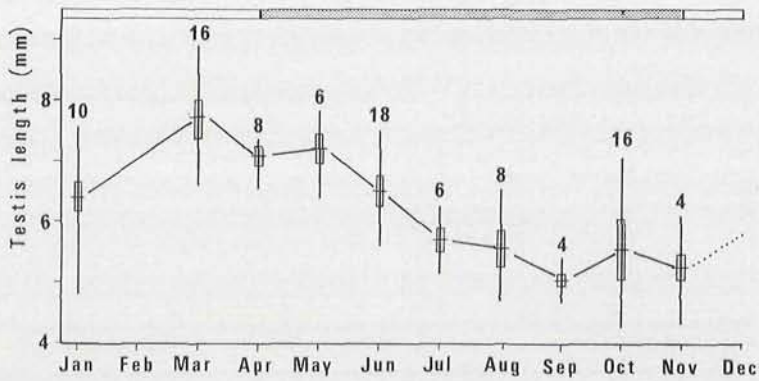


FIG. 1—Mean monthly testis length of *Leiopisma suteri*. Vertical lines, range; numbers, no. of measurements; rectangles, standard deviation; horizontal lines, mean; shading, period over which epididymes swollen (specimens from Cable Bay and DSIR Coll.).

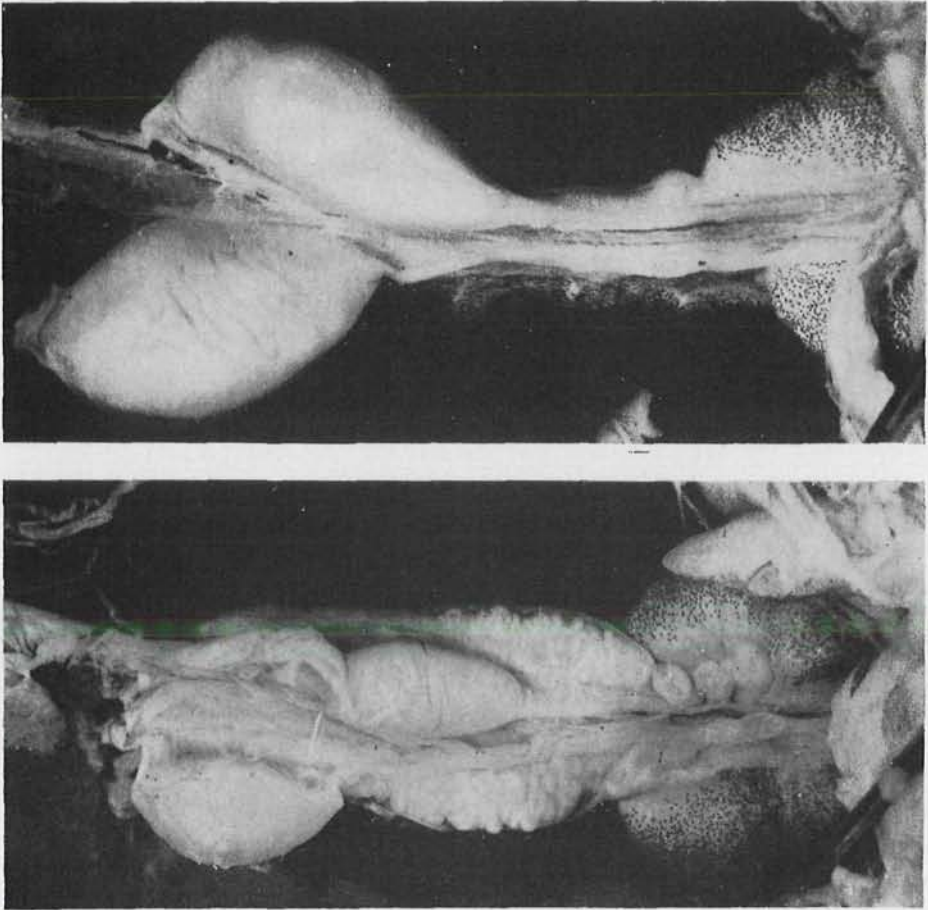


FIG. 2—Testes and epididymes of *Leiopisma suteri*: (upper) 19 Jan. 1972 – enlarged testes and small epididymes; (lower) 17 Sep. 1972 – small testes and turgid epididymes. Scale: width = 20 mm approx. (Photos: G. W. Batt)

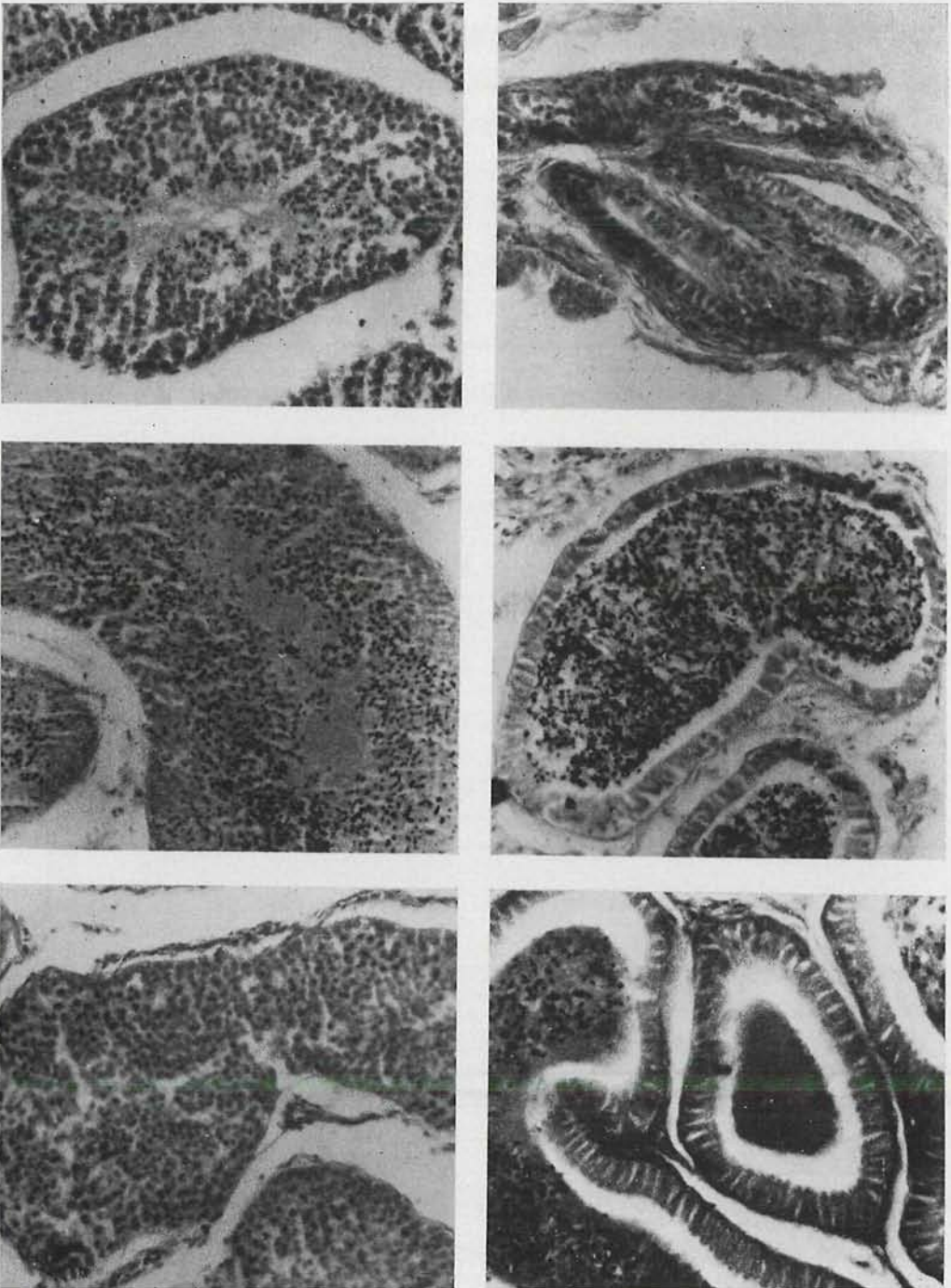


FIG. 3—Sections through testes (a,c,e) and epididymes (b,d,f) of *Leiopisma suteri*: (a,b) January. The seminiferous tubules (a) are beginning production of sperm and spermatids, which are present around the lumen. Sperm have not reached the epididymes (b), which are still atrophied. (c,d) April. Spermatids and sperm are present in each seminiferous tubule (c) and within the swollen epididymes (d). (e,f) November. Spermatids are absent from the seminiferous tubules (e), but some spermatids and sperm are still present in the epididymes (f), which contain much cell debris. Scale: field width = 0.6 mm.

Males with swollen epididymes were first captured in April. By May the testes were smaller, and the seminiferous tubules were still visible, but compacted. The seminiferous tubules remained compacted in appearance and the mean testis length continued to decrease until September, by which time the epididymes were greatly enlarged (Fig. 2b). Increase in testis length began in November, and by January the seminiferous tubules were distended but had not become fully turgid.

Fluctuation in testis size throughout the year is not great, the mean maximum being 7.7 mm and the mean minimum 5.0 mm. The range from absolute maximum to absolute minimum spans 4.6 mm (8.8–4.2 mm). At no stage do the testes become clear, as was described by Mayhew (1965, 1966a, b) for three species of *Uma* (Iguanidae).

Sections through the testes and epididymes show a cycle of sperm production reflected in the macroscopic changes to these organs (Fig. 3). In January the first spermatids appeared in the seminiferous tubules; the epididymes were atrophied and their lumina empty (Fig. 3a,b). By March, when the testes were at their largest, spermatids were the most abundant cells within the seminiferous tubules, and from April until July the testes and epididymes contained abundant spermatids and sperm (Fig. 3c,d). Spermatids were far fewer in the seminiferous tubules in August, but were still abundant in the epididymes. By November spermatids had disappeared from the seminiferous tubules, which were undergoing spermiogenesis for the next season, but were still present in the epididymis along with cell debris (Fig. 3e,f).

FEMALE CYCLE

The ovaries lie posterodorsally in the body cavity, the right ovary being slightly forward of the left ovary. A yellow adrenal body lies dorsal to each ovary. The oviducts are attached to the peritoneum behind the lungs, the ostia tubae facing vertically (Fig. 4c). The oviducts each have a separate opening in the urodeum of the cloaca.

CORPORA ALBICANTIA

Associated with the ovaries of many lizards are bodies of one of three types: corpora lutea, corpora albicantia, and corpora atretica. Corpora atretica are degenerate follicles, which in *Takydromus tachydromoides* (Lacertidae) are yellow (Telford 1969). Apparently they do not persist for long, and none was identified in any specimen of *L. suteri* examined in the present study.

Corpora lutea are produced at ovulation, and in oviparous lizards degenerate soon after laying (Tinkle 1967, Mayhew 1968). Usually they are described as being doughnut-shaped, and may range in colour from red to cream or white (Telford 1969). Telford found that the corpora lutea deepened in colour as they regressed, finally turning bright orange, at which stage he named them corpora albicantia. In *Takydromus* these apparently persist for life (Telford 1969).

Compressed white bodies (about 0.5 mm in diameter) of granular appearance were often present in the ovaries of *L. suteri*, usually not more than four occurring in each individual. They were found at all stages of the ovarian cycle, and appeared to persist for most of the year. However, they bore no resemblance to the corpora lutea described in the literature. Because of the relatively long period for which they persisted and the fairly constant number per ovary, I have regarded them as corpora albicantia. These structures were most common from January to May, when most of the females examined contained three or four. After May they appeared to decrease in number, most individuals containing about two until ovulation. This reduction probably occurred because of the sudden increase in ovary size before ovulation, when the enlarging follicles stretched the tunica of the ovary,

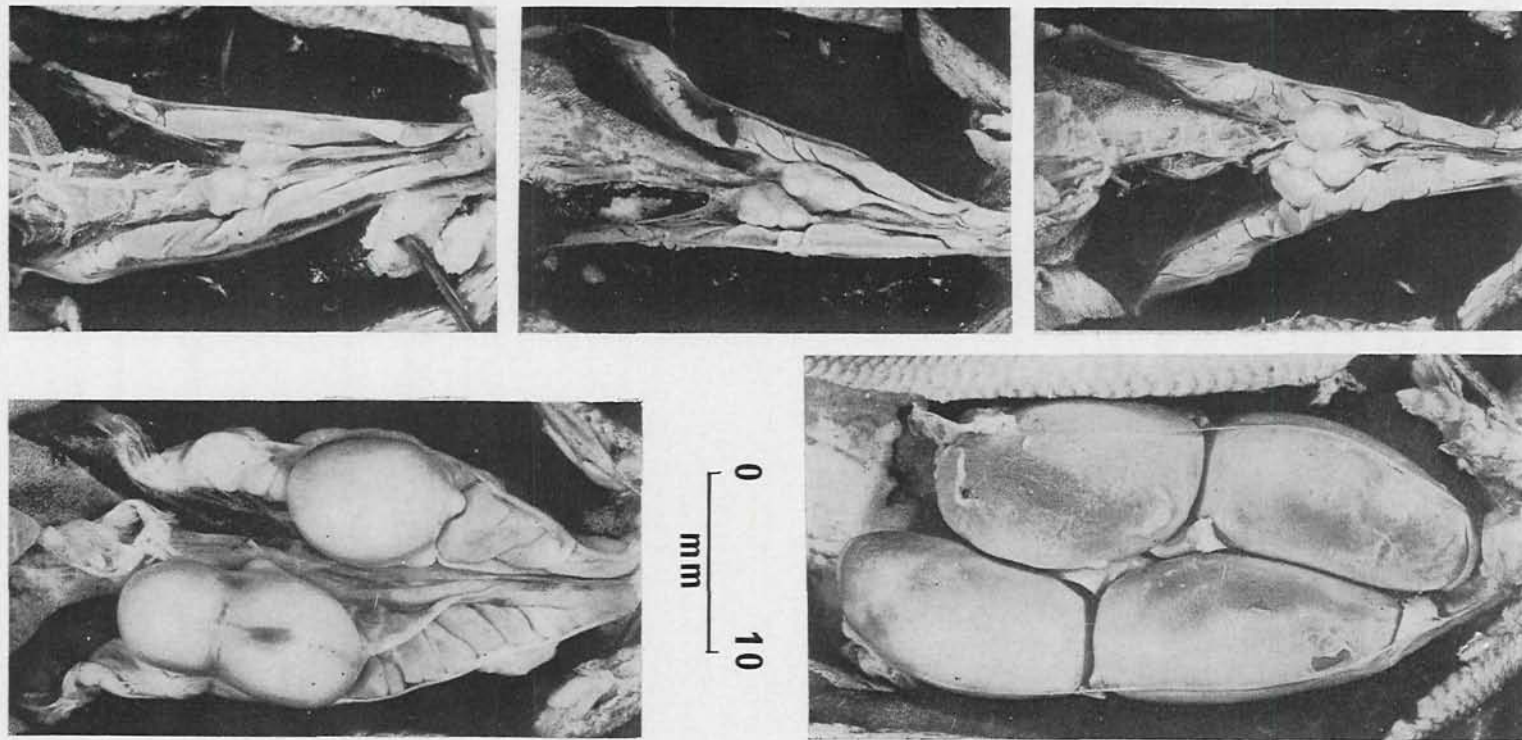


FIG. 4—Seasonal changes to the follicles and eggs of *Leiopisma suteri*: (a) 22 Dec. 1971 – probably soon after oviposition; (b) 26 Feb. 1972 – little change from (a); (c) 7 Jul. 1971 – 3 follicles enlarging more rapidly than the rest. [As the ovarian follicles increase in size, the ovary forms a pouch in the medial wall of the oviduct. The ostia tubae are visible at the anterior end of each oviduct]; (d) 11 Oct. 1972 – 3 follicles appear to be close to ovulating; (e) 6 Nov. 1971 – 4 large oviduct eggs.

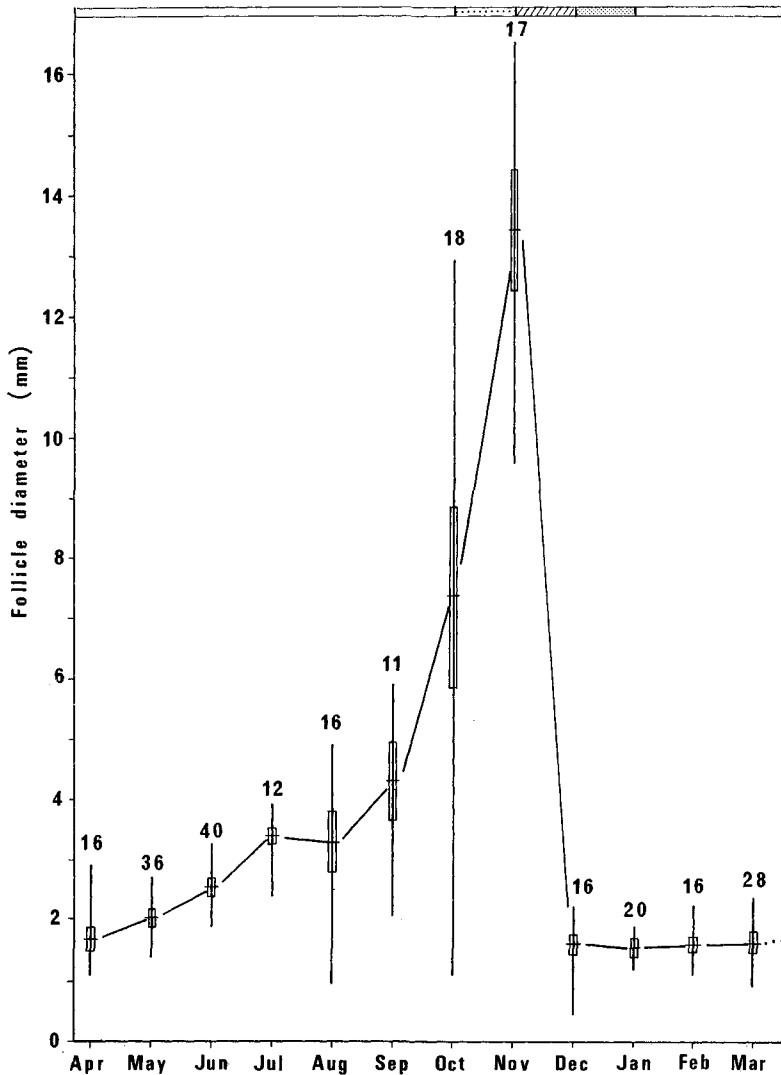


FIG. 5.—Mean monthly follicle and (Nov.) oviduct egg measurements of *Leiopisma suteri*. Conventions as in Fig. 1, except: unshaded, ovarian follicles developing; stipple, ovulation; cross-hatching, oviduct eggs; shading, oviposition.

causing some of the corpora albicantia to dissipate. They were therefore useful as an indicator of clutch size only from December to June.

DEVELOPMENT OF FOLLICLES AND EGGS

Throughout the summer, ovaries from adult females had a flaccid appearance (Fig. 4a,b), and ova were visible within the follicles. The ovaries remained relatively unchanged until May, when the follicles became turgid and their diameter increased. Increases in follicular diameter continued throughout the winter, eventually resulting in the formation of a pouch for the ovary in the medial wall of the oviduct. By July a few follicles (usually the most ventral) were larger than the rest (Fig. 4c). There was little increase in size during August, but

TABLE 2—Numbers of enlarged follicles or oviduct eggs from *Leiopismia suteri*

	SV (mm)	No. of enlarged follicles		No. of eggs	
		L. ovary	R. ovary	L. oviduct	R. oviduct
Sep.	82	2	2		4
	71	3	2		5
	77	2	1		3
Oct.	78*	3	1		4
	80*	2	1		3
	85*			2	2
	105*	0	6		6
	75	1	2		3
	75	2	1		3
	91	2	2		4
Nov.	73			2	2
	73			2	2
	74			1	2
	76			1	2
	78			1	2

* DSIR Coll. (Hen and Chickens Group and Bream I.)

by mid September some of the largest follicles appeared to be close to ovulation, and in most of the females the abdomen was distended and brightly coloured.

The first oviduct eggs appeared in October, and all adult females examined in November had eggs in the oviduct. During October and November the oviduct eggs grew rapidly, until at the time of laying they were about 13.5 mm long, having been somewhat elongated by pressure of the tubular oviduct (Figs 4e, 5). After deposition several turgid follicles were still present in the ovary. These probably regressed throughout the summer, since all individuals dissected in March contained transparent follicles with visible ova.

OVIPOSITION

The time of oviposition was inferred from the sudden decrease in the number of gravid females in the Cable Bay population. When the area was visited on 11 December 1971 gravid females were numerous, but on the next visit (22 December) no captured females contained eggs. Three gravid females in an outdoor cage (Townes 1975) deposited their eggs between 21 December 1971 and 6 January 1972, and the stomach contents of a female captured at Cable Bay on 22 December included a lizard egg.

These data indicate a laying period at Cable Bay for the 1971 season from mid December to early January, slightly later than the oviposition period of late November or December suggested by Whitaker (1968a). No nests were found at Cable Bay, despite careful searching. It is assumed that the skinks deposited their eggs in surroundings similar to those described by Whitaker (1968a). At Cable Bay, the most suitable nesting region appeared to be near the edge of the doab (*Cynodon dactylon*), where gravid females were common during November and December.

Two gravid females were captured at Cable Bay between 26 January and 2 February. Both were small individuals (one of 67 mm SV), and were probably close to oviposition, as suggested by the presence of two eggs in a pitfall trap set over the same period at the edge of the doab.

CLUTCH SIZE

Clutch size was estimated from counts of oviduct eggs and large follicles (from September to November). Corpora albicantia were considered to be insufficiently consistent for

estimating previous clutch size, since many appeared to dissipate towards ovulation. Counts of oviduct eggs and enlarged follicles gave a mean clutch size of 3.7 (Table 2).

HATCHING

The hatching period was estimated indirectly from the appearance of hatchlings in the population. In 1971 one hatchling was found at Cable Bay on 20 March, and when the area was next visited (21 April) they were abundant. In 1972 no hatchlings were seen on 21 February at Cable Bay; the first were captured on 8 March. Several were seen at Boulder Bay, Rangitoto Island, on 18 March, and hatchlings were abundant at Cable Bay when the area was visited on 8 April. One small hatchling (34 mm SV), presumably from eggs deposited between 21 December and 6 January, was found in the outdoor cage on 18 April.

At hatching, *L. suteri* is 32–36 mm SV (Whittaker 1968a). Most of the lizards of this size appeared in Cable Bay catches between March and April, though a few were taken several months later, including one of 36 mm SV caught in August 1971.

GROWTH

SIZE CLASSES

Size frequency distributions (Fig. 6) indicate the growth rates of young lizards up to the end of their second hibernation (18 months of age), when overlap between adjacent age classes became apparent.

Lizards at Cable Bay were divided into three major (and one minor) groups (Fig. 7a). Hatchlings were arbitrarily defined as the smallest lizards in the population. When a group of hatchlings began to appear, those of the preceding year were classed as juveniles. Thus, young lizards are hatchlings for no more than 12 months, and may be up to 60 mm SV, the size range overlapping that of the juveniles. Juveniles (53–70 mm SV) include a small transitional subgroup, the subadults, which are late-breeding individuals of 67–70 mm SV. In view of the later oviposition time of this group, it is considered to comprise precocious juveniles rather than slow-growing adults. Size differences between individuals hatched in the same year are extremely important in this respect. The size range of six hatchlings marked in December 1971 spanned approximately 7 mm SV, and in some individuals the difference had increased within a few months: in December, skink No. 80 was 50 mm SV and No. 30 was 54 mm SV; by July 1972, No. 80 was 55 mm SV and No. 30 was 64 mm SV. At that rate of growth, No. 80 would mature in its third season and No. 30 in its second.

SIZE AND AGE AT MATURITY

Age at first breeding was calculated from recaptures and size frequency distributions. Assuming that small females depositing late are precocious, the time from hatching to deposition of their first clutch (February, the year after hatching) is 23 months. If, however, they mature too slowly to allow copulation in their second year, first deposition will occur in the following December, 33 months after hatching, at about 72 mm SV. An example of this was skink No. 150, recaptured on 21 April and 25 July 1971 at 64 mm SV, and again on 28 August 1972 at 72 mm SV, and showing the bright orange ventral colouring of breeding condition. It is probable that most males also reproduce for the first time three winters after hatching, i.e., at about 29 months of age and 70 mm SV.

The smallest female found containing oviduct eggs was 67 mm SV, and the smallest male found from dissection to contain swollen testes was 68 mm SV. In almost all other

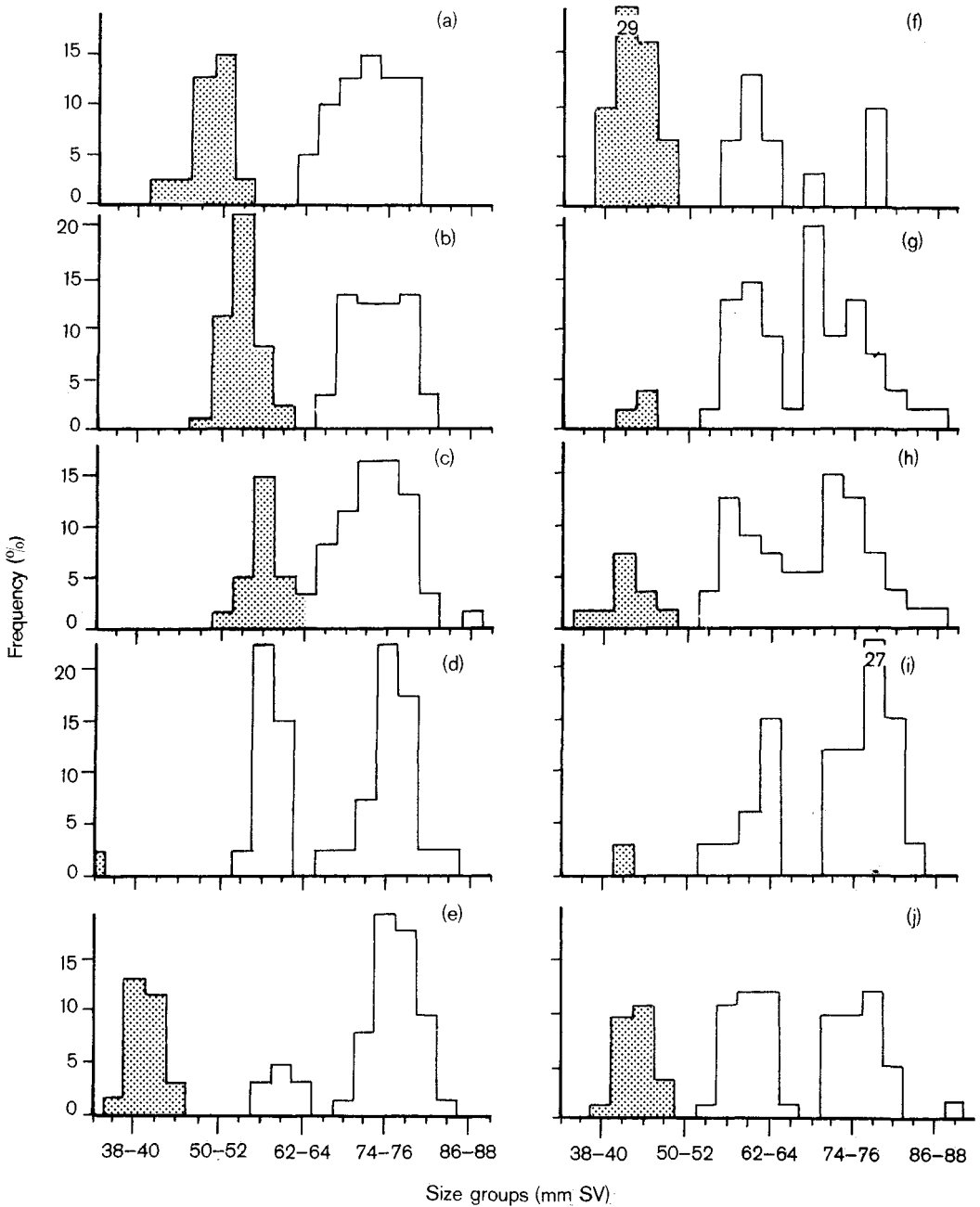


FIG. 6—Monthly size frequency distributions of hatchling (shaded), juvenile, and adult *Leiopismis suteri* at Cable Bay, illustrating rapid growth of hatchlings from November to March and slow growth of each size class between April and October: (a) Nov. 1971 ($n = 41$); (b) Dec. 1971 (91); (c) Jan. 1972 (59); (d) Mar. 1972 (40); (e) Apr. 1972 (61); (f) Jun. 1972 (31); (g) Jul. 1971, 1972 (56); (h) Aug. 1971, 1972 (56); (i) Sept. 1972 (33); (j) Oct. 1972 (83).

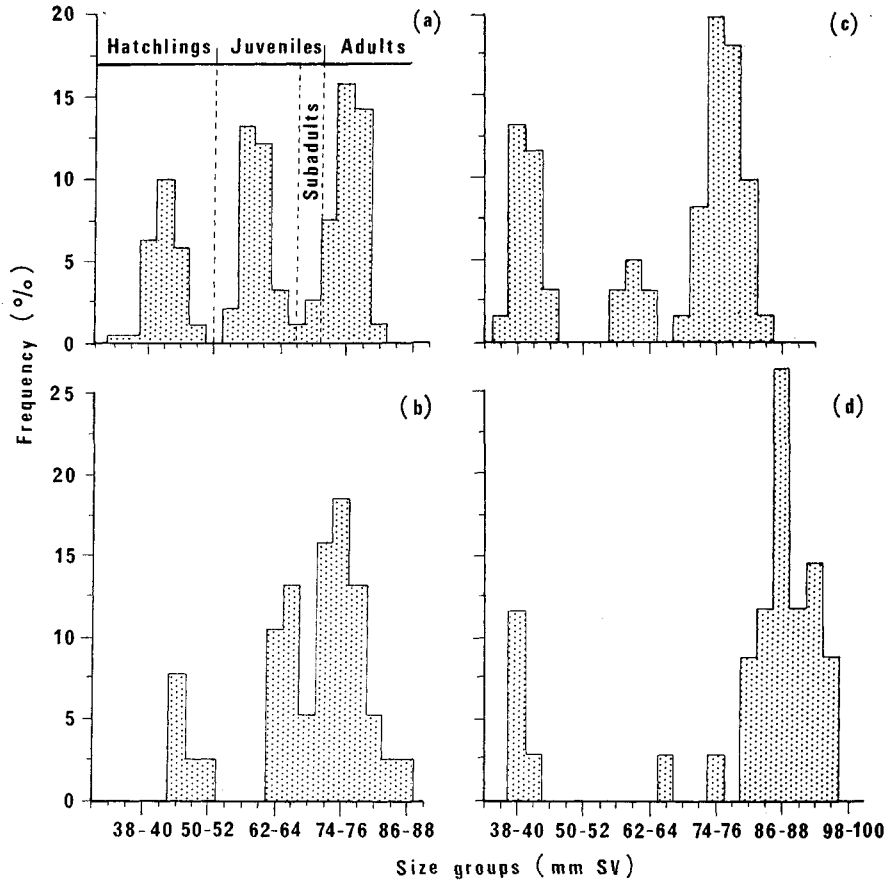


FIG. 7.—Size frequency distributions, showing size classes of *Leiopisma suteri*: (a) Cable Bay, Mar.–Aug. 1972 ($n = 190$); (b) Waiheke I., Nov. 1971 (38); (c) Motutapu I., Apr. 1972 (61); (d) Cuvier I., May 1972 (34).

Cable Bay captures, gravid females, skinks with adult coloration, and males with swollen hemipenes were over 70 mm SV.

The mean size at maturity for the Cable Bay population was 79 mm SV, the greatest number of adults falling into the 74–76 mm group (Fig. 7a). These measurements also occurred in *L. suteri* populations sampled near Motutapu Island, e.g., at Waiheke Island (Fig. 7b). Only rarely were *L. suteri* larger than 85 mm SV captured in either area. Adults beyond the vicinity of Motutapu tended to be larger, however (the biggest specimen dissected was a male of 107 mm SV from Bream Island). This held true for all populations sampled away from the inner Hauraki Gulf, i.e., adults on Rangitoto, Motutapu, and Waiheke Islands were smaller than those from other populations. This is exemplified by comparing the size distributions of *L. suteri* from Cuvier Island and from Motutapu (Fig. 7c,d). Similarly, 6 adults captured on Burgess Island (Mokohinau group) averaged 91.5 mm SV (range, 82–101), 7 from the Aldermen Islands (Towns & Hayward 1973) averaged 94 mm SV (range, 86–102), and 44 from the Poor Knights Islands averaged 87.5 mm SV (range, 70–105; Whitaker 1968b).

DISCUSSION

The differences in mean adult size of *L. suteri* between Motutapu and Waiheke Island populations and populations from outside the Hauraki Gulf pose an intriguing problem. According to Carlquist (1965), reptiles are particularly sensitive to island conditions; numerous instances of gigantism and dwarfism are known, for example. There are several possible reasons for the presence of larger *L. suteri* away from the inner Hauraki Gulf. First, temperatures on outer offshore islands are often milder than at mainland coastal stations in the same latitude (Carlquist 1965). This could increase foraging times, since winter limits on foraging are probably due to low night-time temperatures. It would also lengthen the growing season. *L. suteri* shows a marked decrease in growth rate over the winter at Cable Bay, and this may be less obvious in warmer areas. Second, outer islands are more exposed to storms, so arthropods associated with storm-tossed seaweed are perhaps more readily available. Third, it is possible that the smaller animals at Motutapu reflect a higher rate of population turnover, because they occupy a marginal habitat near the southern limit of the species' range (Towns 1974).

Detailed information on the timing of the male cycle of skinks is lacking, so comparison of the male reproductive cycle of *L. suteri* with other species' must rest on meagre data. Nevertheless, it appears from the literature that there are several types of lizard testicular cycle (from comparison of macroscopic measurements of testis length, the state of the epididymes, and histological sections). In the first type (e.g., *Anolis carolinensis*; Iguanidae), full breeding condition appears to occur at approximately the same time as maximum testis volume (Licht 1967). This has been described for other iguanids by Mayhew (1965, 1966a, b) and Mayhew & Wright (1970) for various species of *Uma*, and by Marion & Sexton (1971) and Goldberg (1974) for *Sceloporus* spp. In a second type of cycle, maximum testis size does not necessarily correspond with maximum sexual activity. Maximum sperm content in the seminiferous tubules of the tropical Australian skink *Leiopisma fuscum* is reached 1–2 months after the testes reach maximum volume (Wilhoft & Reiter 1965). *L. zelandicum*, with sperm still present in the epididymes after the testes have reached minimum size (Barwick 1959), and *L. suteri*, with sperm in the epididymes during retrogression of the testes, also fit into this group.

The cycles can also be divided on the basis of duration of reproductive activity. *Leiopisma fuscum* has a short reproductive period, sperm occurring in the epididymes for only 2 months. In contrast, *L. rhomboidalis* (from the same area) is capable of reproduction throughout the year (Wilhoft 1963); *L. zelandicum* has sperm in the epididymes for 6 months; and *L. suteri* for at least 7 months.

Wilhoft (1963) suggests that the main factor limiting the timing of reproduction in *L. rhomboidalis* is cold, during which the females are at low productivity. An important limit on the reproductive behaviour of the skinks of temperate New Zealand is the cold winter period, although the reproductive organs may be histologically active at this time. Winter inactivity would probably restrict the mating period of *L. zelandicum* to 3 months between January and April (summer–autumn), and that of *L. suteri* to 4 months from August to November (late winter–spring).

Although *L. zelandicum* is viviparous and *L. suteri* oviparous, the duration of each part of the female cycle is similar, and in both species ovulation probably occurs in late September or early October. Based on the reasonable assumption that fertilisation occurs within the oviducts [i.e., after ovulation), female *L. zelandicum* would have to store the sperm over the winter months, as was tentatively suggested by Barwick (1959). Since

Atsatt (1953) first reported sperm storage in female chameleons, the phenomenon has been found in members of the families Iguanidae, Gekkonidae, and Eublepharidae (Cueller 1966) and the skink *Hemiergis peronii* in Australia (Smyth & Smith 1968, Smyth 1968). The limited winter activity of *L. suteri* would probably have the effect of restricting copulation to the pre-ovulation period in spring, thus rendering sperm storage for long periods unnecessary.

The number of eggs laid in one clutch by females of many lizard species increases with the size (and hence, usually, age) of the individual (Tinkle 1967, Tinkle *et al.* 1970). There is no evidence for consistently larger clutches in large female *L. suteri*. Small, precocious females depositing their first clutch appear to produce as many eggs as do larger adults, but to lay them a month later. Assuming that these eggs have the same incubation period as clutches laid earlier, the total hatching period would last from March to April; this would explain in part the long period over which hatchlings appeared at Cable Bay. Late eggs produced by precocious females would be less likely to survive the early onset of winter conditions.

Clutch size is similar in the three New Zealand species so far studied: *L. zelandicum* produces three to five young (Barwick 1959), *Sphenomorphus pseudornatus* (= *Leiolopisma pseudornatum*; Greer 1974) two to four young (Fawcett 1964), and *L. suteri* three to four eggs. The main differences between *L. suteri* and the other two species are in the form and duration of development of the eggs. Both *L. zelandicum* and *L. pseudornatum* have gestation periods of approximately 3 months, whereas *L. suteri* retain their eggs in the oviducts from late October or early November until late December (2 months). Incubation (at Cable Bay) then takes a further 3 months, until March, a total development period of 5 months. This differs markedly from other skinks studied; the family as a whole tends to have a short incubation time by comparison with other lizards. Tinkle (1967) suggests that this is because of the tendency of Scincidae to retain eggs in the oviduct, depositing them when embryonic development is advanced. An extreme example is *Siaphos equalis*, which lays its eggs a few days before they hatch (Cogger 1967, Bustard 1970).

Considering the differences between the reproductive habits of *L. zelandicum* (viviparous, with placentation) and of *L. suteri* (oviparous, with an exceptionally long incubation period), it may be pertinent to question the inclusion of these two species in the same genus. Unfortunately, perhaps, classifications of the Scincidae by Boulenger (1885), Smith (1937), Mittleman (1952), and Greer (1970, 1974) have been based on skeletal or external morphological characters, and have often resulted in a mixture of viviparous and oviparous species within one genus. Fitch (1970) implies that Mittleman's more restrictive classification may have permitted inclusion of many of the oviparous forms of Smith's (1937) genus *Leiolopisma* in *Lampropholis*, so that "some or all" of Mittleman's *Leiolopisma* are viviparous (Fitch 1970, p. 83). However, Fitch overlooked *L. suteri*, which was placed by Mittleman (and later Greer (1974)) in *Leiolopisma*. Whichever classification is used, the result is still a mixture of oviparous and viviparous species in this genus.

It has been suggested that the high proportion of ovoviviparous and viviparous species within the New Zealand lizard fauna is the result of low temperatures during the Pleistocene ice ages causing selection against oviparity (Robb 1973). It is therefore surprising that *L. suteri*, being oviparous, should have such a long incubation period, and also that it should be nocturnal. *L. suteri* generally ceases foraging at temperatures below 10°C (Towns 1975). If it occupied a geographic range in the late Pleistocene similar to its present distribution, the maximum/minimum temperatures for the warmest month (January) would have been 7.7°C to 13.3°C (Robb 1973), on which basis feeding would be impossible for most of the

year. This leaves the possibilities either that late Pleistocene temperatures in Northland were warmer than is suggested for the rest of New Zealand, or that the present distribution of *L. suteri* is the result of post-Pleistocene movement from further north (precise data on Pleistocene palaeoclimate for Northland are lacking; J. A. Grant-Mackie, pers. comm.). Either possibility would explain the otherwise anomalous position of *L. suteri* in the postulated scheme of evolution of New Zealand's skink fauna.

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