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## Ecology of the black shore skink, *Leiopisma suteri* (Lacertilia: Scincidae), in boulder beach habitats

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The ecology of the nocturnal black shore skink, *Leiopisma suteri*, was studied on a boulder beach at Cable Bay, Motutapu Island, for 19 months. Distributions over a stable beach (Motutapu Island) and an exposed beach (Cuvier Island) were compared, and the effects of storms on the Cable Bay population were noted. Density, aggression, thermal preference, feeding, and fat reserve fluctuations were also studied. The *L. suteri* population at Cable Bay has, in favourable areas, one of the highest densities (13/m<sup>2</sup>) recorded for a lizard species. Spatial distribution of this population varies between the different age classes: adults congregate in the most stable areas, whereas hatchlings are commonest in the least stable areas. Storms cause changes in the beach structure and in the spatial limits of the population.

### INTRODUCTION

The black shore skink, *Leiopisma suteri* (Boulenger), is a nocturnal lizard found on islands off the coast of north-eastern New Zealand (Townes 1974a, b), where it generally inhabits boulder beaches near high tide level.

Three features of the ecology of this species make it of particular interest. First, it is the only known egg-laying lizard native to New Zealand (Whitaker 1968a). Second, although several New Zealand lizard species occur in coastal areas (Whitaker 1968b, Townes 1972), *L. suteri* is the only one known to be restricted to the shoreline. Third, boulder beach populations of this lizard may reach extremely high densities (Whitaker 1968a, 1973).

Detailed ecological studies have been made of only two New Zealand skink species, *Leiopisma zelandicum* (Barwick 1959) and *L. pseudornatum* (Fawcett 1964; as *Sphenomorphus pseudornatus*), both in wasteland areas. There has been no long-term study of the ecology or life history of *L. suteri*, although there are several distribution records and notes on its habits (Atkinson 1964; Whitaker 1968b, 1973; Fawcett 1971; Townes 1971, 1972, 1974a; Townes & Hayward 1973; Robb 1973). In general the ecology of skinks has received little attention, no doubt partly because of the elusiveness and unspectacular nature of many of these lizards. Except for the work of Alcalá & Brown (1967) and Fricke (1970), few of the studies have been centred on the shoreline habitat.

The present work, part of an M.Sc. thesis study, was undertaken to provide information on the habits and ecology of *L. suteri*, in particular the ways in which a boulder beach population adjusts to the instability of its habitat.

Most of the field work was done over a 19-month period on an isolated boulder beach population of *L. suteri* at Cable Bay, Motutapu Island. This included mapping changes in the vegetation cover, the shape of the beach, and the amount and position of debris under which the lizards could shelter. Landing Bay, Cuvier Island, was visited for 3 weeks in May 1972 to study the distribution of *L. suteri* over a beach on an island more exposed than

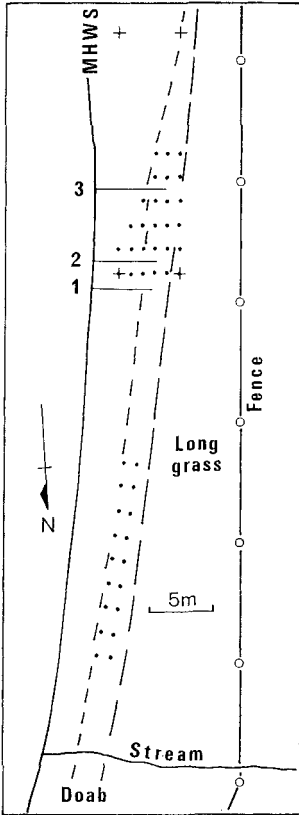


FIG. 1—The study area, Cable Bay, Motutapu Island.

FIG. 2—Sketch map of study area (broken lines, seaward limits of grassed areas; dots, trap grids; +, quadrat corners; 1, 2, 3, transect lines along which lizards were captured at end of study). The *Leiopisma suteri* population was concentrated in the quadrat region, and extended as far north as the stream.

Motutapu. In addition, brief visits were made to Lady Alice Island (Hen and Chickens group), Burgess Island (Mokohinau group), Red Mercury Island and Double Island (Mercury group), and Waiheke Island and Rangitoto Island (Hauraki Gulf).

#### METHODS

An area at Cable Bay in which *L. suteri* was obviously abundant was marked off in a  $5 \times 20$  m quadrat. The area within the quadrat was mapped monthly using a point analysis method, and the data were transferred directly to graph paper. The quadrat was also photographed regularly from two set positions.

Pitfall traps (Whitaker 1967) were buried amongst the boulders on a  $2 \times 1$ -m grid. Initially 36 were set, covering a  $10 \times 5$ -m area within the quadrat, but several of those to seaward were consistently washed out during storms, and so were withdrawn. The 27 traps remaining in the more stable areas were used throughout the study, and a further 18 were subsequently set in 2 rows on a  $2 \times 1$ -m grid 20 m north of the quadrat, where the lizards occurred at a lower density. These 45 traps were set once each month without bait and left for a week. Lizards captured were marked using a toe-clipping method (Tinkle 1967), measured from snout to vent (mm SV), and released beside the trap in which they had been captured.

Observations on behaviour and thermal preference were made in an outdoor enclosure on the biological sciences building roof at Auckland University. The cage was 2 m square with 38-cm-high walls of weather-proofed hardboard. The walls and floor were covered with heavy plastic sheeting to prevent the animals from escaping, and the top of the enclosure

was covered with wire netting (30-mm mesh) on a movable frame. Stones and coarse sand covered the plastic on the cage floor.

Information on changes of body temperature in relation to environmental conditions was obtained by taking the cloacal temperatures of five adult *L. suteri* in the outdoor cage at 2-hourly intervals for 24 hours with a Wesco Shultheis ( $-10^{\circ}\text{C}$  to  $+50^{\circ}\text{C}$ ) rectal thermometer. Rock surface temperatures were measured with a Y.S.I. telethermometer (thermistor), and ambient temperature was recorded continuously on a thermograph in the enclosure.

Stomach contents were analysed quantitatively using a modification of the "volume and weights methods" (Hynes 1950). One dead adult with a stomach judged to be completely turgid was selected, and the stomach contents were evenly spread out to form a circular single layer. The circumference of the circle was then traced on to graph paper and given a value of 100. The stomach contents of other lizards examined were scored against this standard.

## STUDY AREAS

### PHYSIOGRAPHY

The main study area, Cable Bay on Motutapu Island (map reference 442 693, NZMS 1 Sheet N42), is a gently curving boulder beach, largely protected by reefs and exposed only to storms from the east and north-east (Figs 1 & 2). Storm-driven seas wash over the beach with any frequency only during winter. The area behind the beach is grazed by cattle and sheep, which influence the vegetation cover on the beach and hence the invertebrate prey available to the lizards. Introduced predators such as rats do not reach the high population densities found on Cuvier Island.

The beach at Cable Bay consists of greywacke boulders, the largest about 20 cm in diameter, with small (50 mm) stones between them. Between high water level (HWL) and the vegetation covering the rocks is a 2–5-m-wide area where the stones may be covered with layers or strips of decaying seaweed, the distribution and size of which depends on the weather. The region is backed by two bands of vegetation. The most seaward line (1–3 m wide) is formed by a creeping grass, Indian doab (*Cynodon dactylon*); this is replaced rather abruptly to landward by tall herbs, including *Rumex* sp., *Plantago lanceolata*, *Sonchus oleraceus*, *Ranunculus* sp., *Galium* sp., *Lotus* sp., *Taraxacum officinale*, *Paspalum dilatatum*, and *Lolium* sp., with occasional clumps of sedge (*Cyperus ustulatus*), rushes (*Juncus maritimus* var. *australiensis*), and Dead Sea apple (*Solanum sodomaeum*). This area ceases at the fence line, where the main vegetation cover is closely cropped pasture.

The area inhabited by *L. suteri* is covered mainly by boulders to a depth of 30 cm. The boulders rest on sand up to the grassed area, where they become intertwined with roots and shoots and beneath which the soil is a sandy loam.

Landing Bay, Cuvier Island (map reference 278 105, NZMS 1 Sheet N35), is exposed to seas from the south-west to the south-east. Boulders on the beach are up to 1.25 m deep near HWL, but decrease in depth further inland. Succulent herbs and sedges (spp. indet.) are common at the base of the hill backing the beach. The slopes around the beach are lightly grazed by stock. Polynesian rats (*Rattus exulans*) are abundant in the area, and are often seen on the beach.

### CLIMATE

The geographic range of *L. suteri* falls within Garnier's (1958) climatic region 'Northern New Zealand', the only region with a mean annual temperature above  $13^{\circ}\text{C}$ . The summer climate is typified by Garnier's observations for January: settled weather, plenty of sunshine,

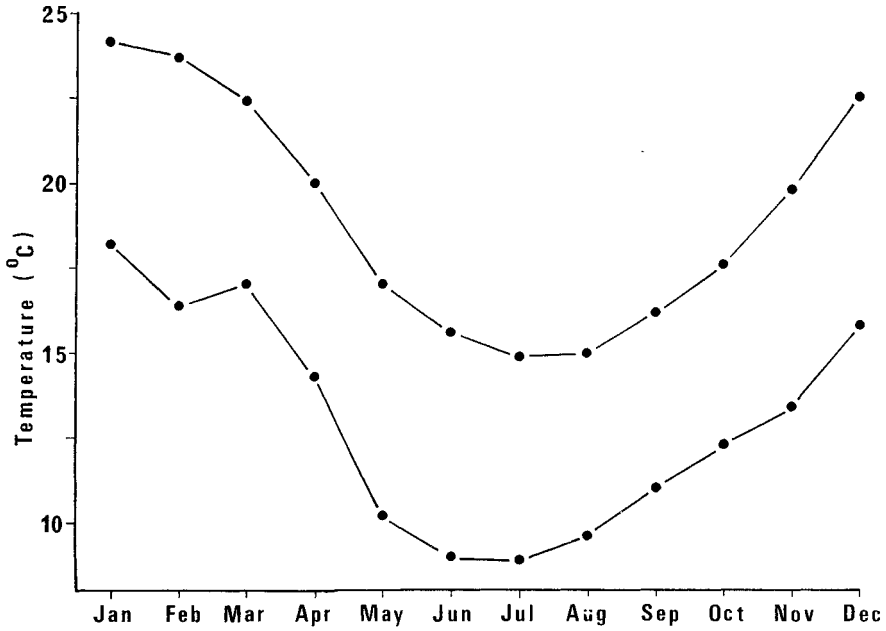


FIG. 3—Auckland City maximum (*upper*) and minimum (*lower*) temperatures for 1970 (data supplied by N.Z. Meteorological Service).

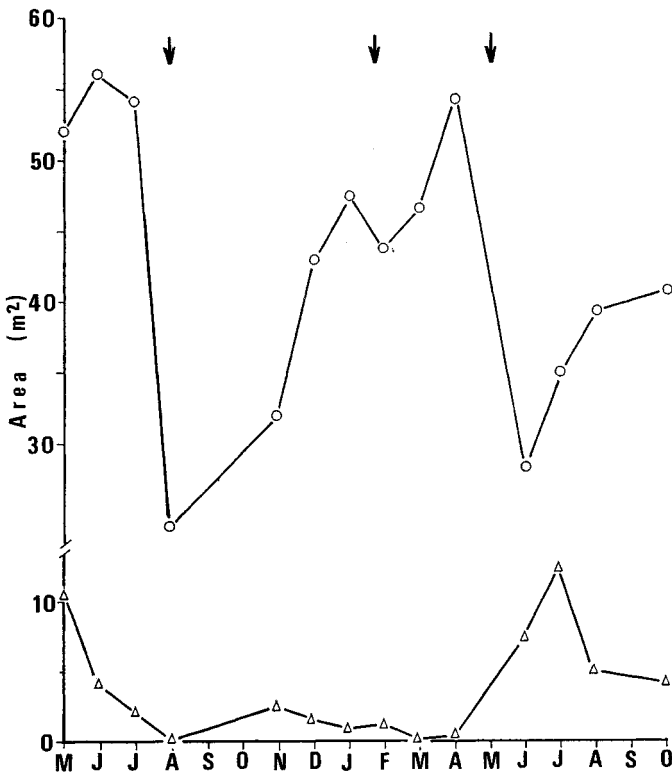


FIG. 4—Changes in area within Cable Bay quadrat covered by seaweed ( $\Delta$ ) and terrestrial vegetation ( $O$ ), calculated from point-analysis maps (May 1971–October 1972). Arrows mark occasions when storms caused sea-wash over the quadrat.

a large diurnal range in temperature, and little rainfall. In contrast, winter is typified by short periods of wet, changeable weather interspersed with several days of sunshine, though diurnal temperature ranges are again large.

Summer temperatures are fairly uniform throughout New Zealand (Garnier 1958), but winter temperatures may have some influence on the range of *L. suteri*, the southern limit of which coincides with Garnier's 50°F (10°C) mean sea-level winter (July) isotherm.

The temperature range encountered by *L. suteri* at Motutapu Island is indicated by the Auckland City maximum and minimum temperatures, recorded 3 km from the study area (Fig. 3).

#### SEASONAL HABITAT CHANGE

Boulder beaches are considered a rather harsh habitat, mainly because of their instability, particularly when the stones are less than 50 mm in diameter (Morton & Miller 1968). This instability is demonstrated by the changes in area covered by terrestrial vegetation and seaweed in the quadrat at Cable Bay (Fig. 4). Major storms (August 1971 and February and May 1972) affected the seaweed less markedly than the vegetation. Changes in the area of vegetation resulted from storm-driven seas washing over the entire habitat, supplemented by the less obvious effects of milder storms. In general this type of change occurred most frequently during winter, and led to degradation of the beach; aggradation occurred in spring and summer. The recovery rate of the vegetation after storm damage was greater in summer than in winter (Fig. 4), in keeping with seasonal differences in plant growth rates.

#### DISTRIBUTION

##### SPATIAL DISTRIBUTION

The most common habitat of *L. suteri* appears to be near seaweed piles on boulder beaches (Hard 1954, Whitaker 1968a, Towns 1972, Towns & Hayward 1973), but populations also occur on rock platforms (Whitaker 1968b), in halophyte communities near the splash zone (Whitaker 1968b; J. Robb, pers. comm.), and on shingle beaches (Whitaker 1973).

The results of three transects on the boulder beach at Landing Bay, Cuvier Island, show *L. suteri* to be present over most of the beach, from the high water line to the start of the vegetation. Greatest numbers were found 6 m above high water, and the centre of the range was 10 m above high water (Fig. 5b).

Three transects at Cable Bay also showed the population to be most abundant across the open beach, but because the region of available habitat was narrower, the range of *L. suteri* was compressed (Fig. 5c).

Pitfall trapping and hand capture data suggest that the distribution of lizards at Cable Bay varied with their age. Fig. 6 shows that the traps, which could be placed only in stable areas, tended to capture more adults; hand captures on the less stable beach to seaward of the traps were biased towards the hatchlings. However, on Cuvier Island this spatial stratification of age classes was not apparent, since very few hatchlings were captured. Age classes of the Cable Bay population are described in detail in Towns (1975).

At least three other skink species are found on boulder beaches within the geographic range of *L. suteri* (Towns 1972), but these usually occur in less exposed areas near vegetation backing the beach. The only northern New Zealand skink with a habitat range similar to that of *L. suteri* is the diurnal, viviparous *Leiopisma smithi*. *L. smithi* was absent from Cable Bay, but occurred sympatrically with *L. suteri* at Landing Bay, where the two species were most abundant on slightly different parts of the beach (Fig. 5a). I have captured *L. smithi* several hundred metres from the coast, whereas *L. suteri* occurs almost invariably near the upper shoreline.

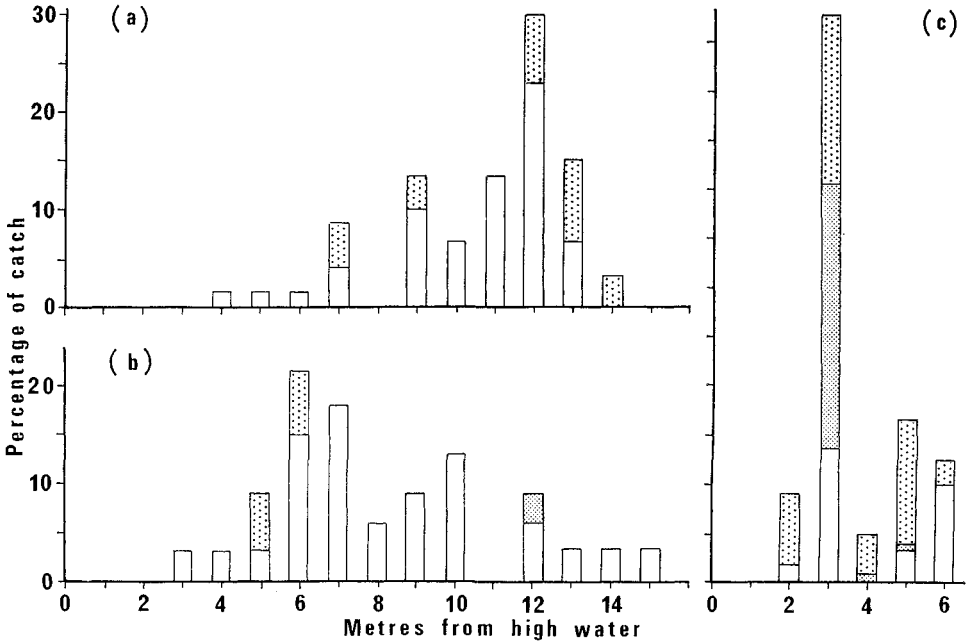


FIG. 5—Distributions of age classes of *Leiopisma smithi* (a) and *L. suteri* (b) over the beach at Landing Bay, Cuvier I. in May 1972, and of *L. suteri* (c) on the more sheltered beach of Cable Bay, Motutapu I. in Oct. 1972 (stipple, hatchling *L. suteri* and juvenile *L. smithi*; shading, juvenile *L. suteri*; white, adults of both species).

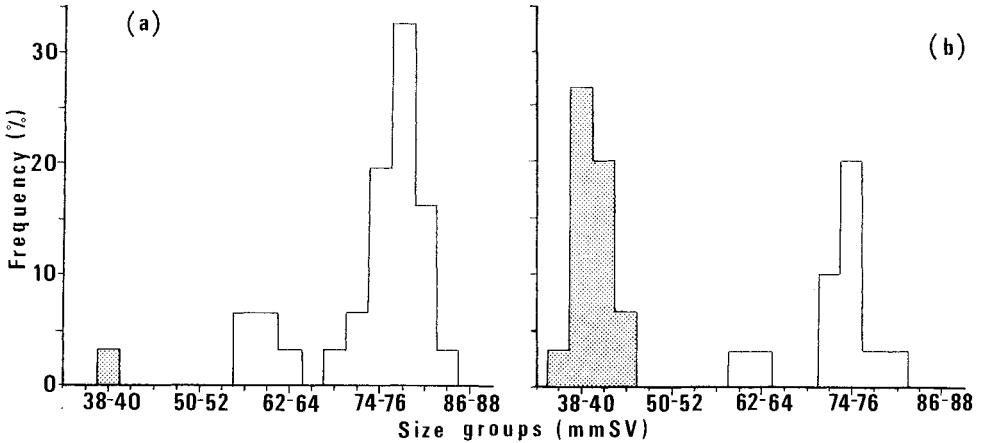


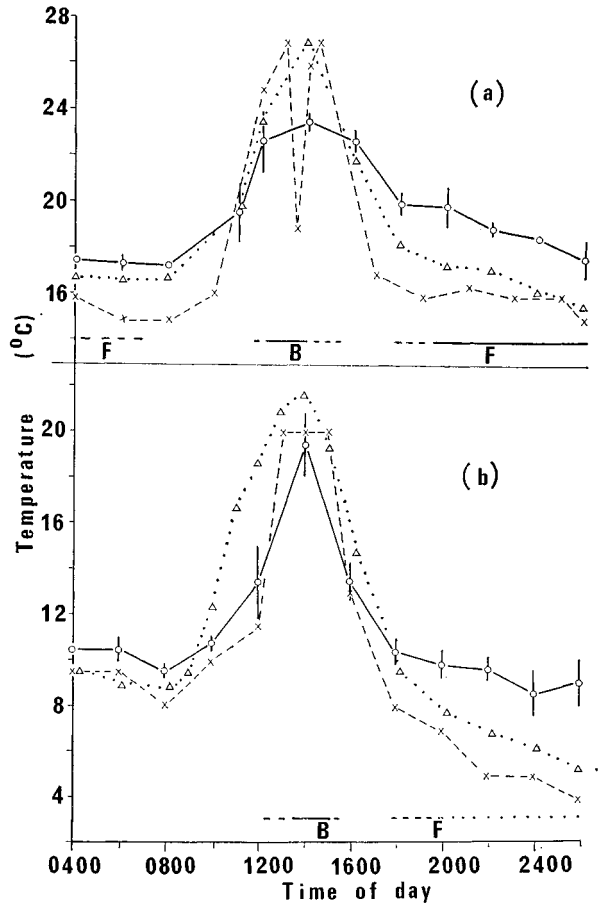
FIG. 6—Size distribution of *Leiopisma suteri* at Cable Bay, Apr. 1972, showing bias of pitfall captures (a) towards adults, and hand captures in marginal areas (b) towards hatchlings (shaded). Sample sizes: (a)  $n = 31$ ; (b)  $n = 30$ .

TEMPORAL DISTRIBUTION

That part of the study area occupied by *L. suteri* at any time could be determined by careful searching. In the long term, changes in beach structure caused by storms led to changes in the size and shape of this range. The more marked changes were of two types, removal of habitat and changes in the nature of habitat, both of which occurred during the May 1972 storm.

Temporal changes in the distribution of *L. suteri* were also related to temperature, seasonal activity, and availability of food (discussed below).

FIG. 7.—Body temperatures of *Leiolo- pisma suteri* compared with environmental temperatures over 24 h, showing effect of substrate as a heat source (particularly between 0800 and 1200) and reduction of foraging time in cool temperatures: (a) 8 May 1970; (b) 20 Jun. 1970 (O—O, mean body temperature of 5 adults; vertical lines, standard deviation (not plotted if <0.3);  $\Delta$  . . . .  $\Delta$ , substrate temperature;  $\times$  - - -  $\times$ , ambient temperature; at graph base — time spent basking (B) or foraging (F) by (solid line) all animals, (broken line) some animals, (dotted line) one only).



## HABITS

### FORAGING

Whitaker (1968b) observed *L. suteri* on Aorangi Island emerging on to rock platforms at about 1930 h (in December) and foraging in the open near rock pools until first light (0430 h). In contrast, all *L. suteri* populations examined in the present study inhabited boulder beaches, and no lizards were observed to be foraging in the open when visits were made at night to the Motutapu and Cuvier Island habitats. It is probable that in these areas most of the lizards' activity occurred within the boulder strand.

### THERMAL ACTIVITY RANGE

There are no records of free-living *L. suteri* basking, but I often observed individuals to be flattened against warm rocks in the outdoor cage. The maximum body temperature recorded was 25°C, though the lizards usually did not allow their body temperature to exceed 24°C before seeking shade. At night, foraging ceased in the cages when body temperatures dropped to 8–10°C (Fig. 7). Below 8°C movements were progressively impaired: one individual found after a frost had a body temperature of 5°C, and was capable only of slow lateral movement of the trunk.

During adverse conditions, especially periods of high temperature, the caged skinks excavated burrows up to 10 cm long. Occasionally these were shared by two or three



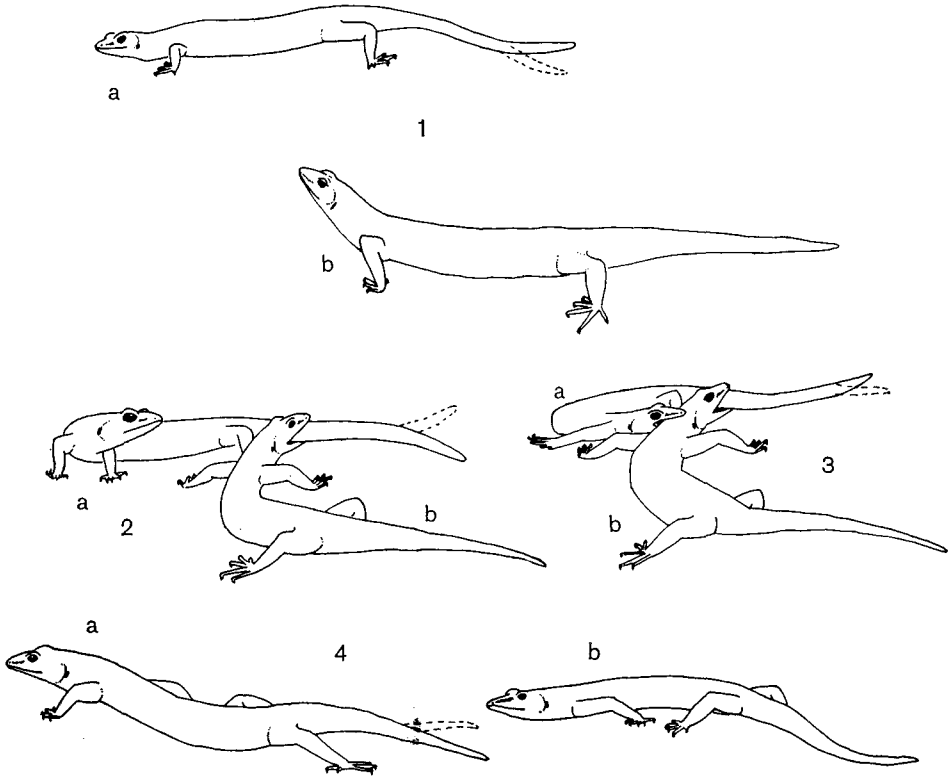


FIG. 8—A typical combat sequence (from sketches of fighting by ♂ *Leiopisma suteri*): 1, opponents sight each other and lower-ranked animal a begins to vibrate tail; 2, higher-ranked lizard b bites a (tail still vibrating) at tail base; 3, a causes b to release tail by biting b across neck; 4, a flees, tail still vibrating, pursued by b.

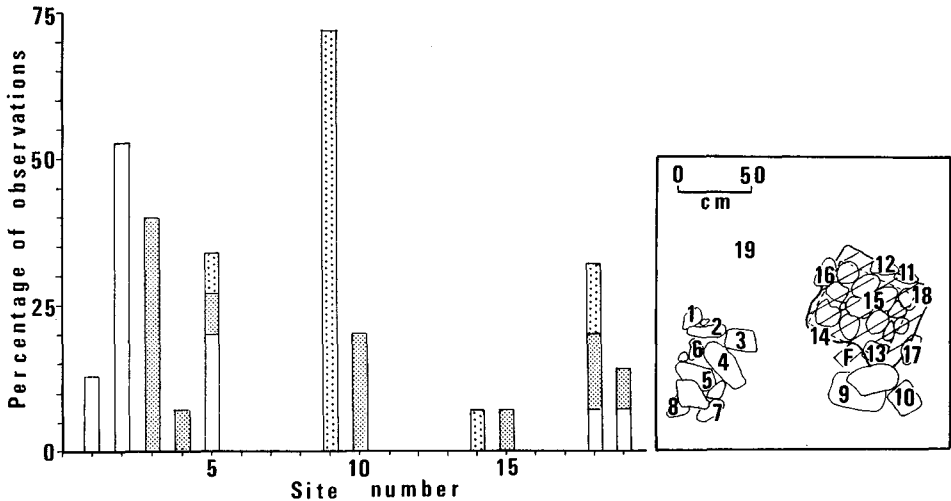


FIG. 9—Homesite preferences of 3 ♂ *Leiopisma suteri* (differential shading) in an outdoor cage (inset) from 15 daytime observations over 2 months (Jul.–Sep.) (numbers: potential homesites beneath stones except 14, under a glass sheet on sand; 15, among stones under sack (cross-hatched); 18, inside sack; 19, away from rock cover; F, food container).

individuals (sex unknown). One such burrow, containing several *L. suteri*, was found in summer under a stone at Cable Bay.

The seaweed under which *L. suteri* would normally be found at Cable Bay became saturated with rainwater during the winter, forming a cold sludge which dripped on to the rocks below. Mid-day temperature recordings for one day in July showed wet seaweed to be approximately 4.0°C colder than the drier substrate under rocks. Under these conditions lizards were absent from the seaweed, and were instead associated with drier rocks near the seaweed piles.

#### ORGANISATION OF THE POPULATION

##### AGGRESSION AND DOMINANCE

Among the Scincidae, combat is often introduced by slow vibration of the tail (Fitch 1954, Fawcett 1964), and *L. suteri* shows agitation in this way. Fighting, which was common between caged males, took a rather stereotyped form (Fig. 8); usually the same animal was submissive in each observed encounter between two particular individuals. In the field, captured *L. suteri* were often found to have scars about the head and neck, and occasionally across the body. These scars were most obvious at the beginning of the breeding season, and were probably caused by fighting. Loss of toes and parts of the tail were also attributable to combat; in the outdoor cage, for instance, the tip of the tail of one individual had been chewed, and appeared raw for much of the summer. Regeneration began in winter, when activities were restricted. Combat, together with movement of the boulders, is probably the cause of the high proportion of adult lizards captured at Cable Bay having regenerated tails — this amounted to 67% of females and 82% of males (data from 57 lizards captured for dissection).

The form of combat shown by male *L. suteri*, with one individual consistently ranked above others, suggests a typical dominance hierarchy. In the outdoor cage (where three males were observed for several months) this hierarchy extended from chance meetings, when the lower-ranked animal would flee, to a hierarchy of homesites and basking sites. The highest-ranked animal had its homesites close to the food container and in the section of the cage warmed first by the sun. The lowest-ranked lizard (the individual with the chewed tail) had its homesite in the section of the cage warmed last by the sun, and was never found near the homesite of the top-ranked animal. None of the male lizards occupied a given homesite at the same time as another male (Fig. 9).

A detailed study of the relationship of females to the hierarchy of males was not attempted because of difficulties in accurately sexing more than a few individuals. However, no known females were observed fighting, and females released in the outdoor cages shared homesites with males.

##### MOVEMENT

Generally the organisation of animal populations is described in terms of territory, social hierarchy, or home range (Marler & Hamilton 1968, Brown & Orians 1970). Trapping in the present study was designed to find which of these three concepts best described the behaviour of *L. suteri*. However, after 19 months' trapping it was found that pitfalls provided little useful information on movement of individuals; the average time required to capture animals more than twice was 4.7 months ( $n = 15$  lizards), and the apparent movement was only a few metres. In one instance 8 months elapsed between the first and third captures. Over such a period the individual may have moved over a large area, even though the movement revealed by trapping in this example was only 2 m.

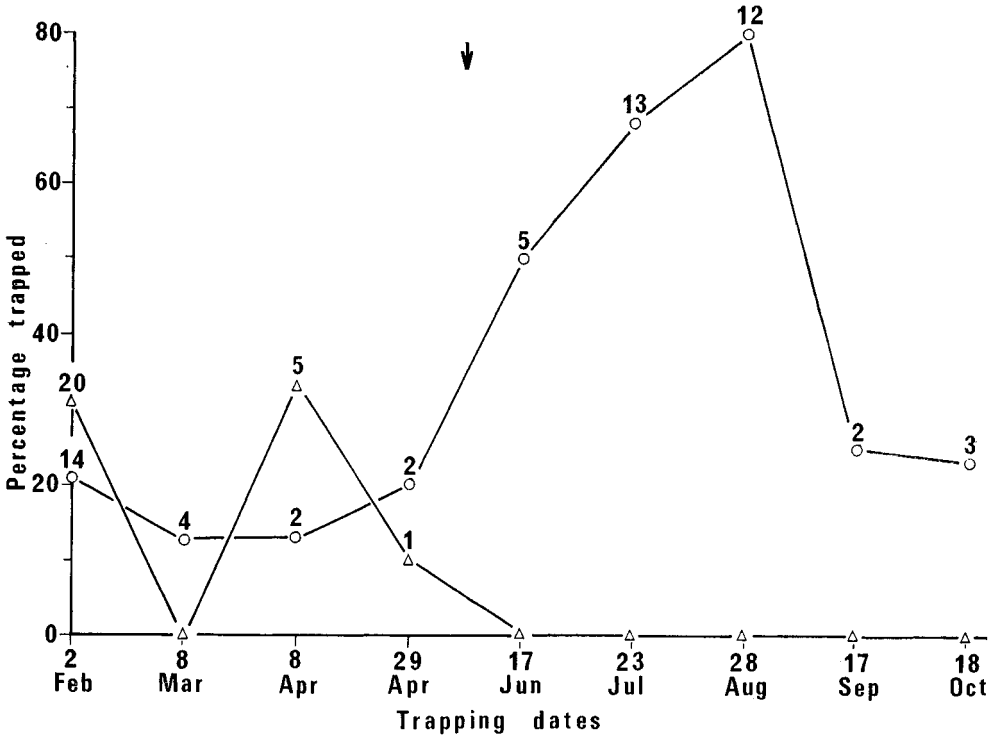


FIG. 10—Numbers of *Leiolopisma suteri* captured in 2 pitfall traps 10 m apart at Cable Bay on trapping dates before and after a major storm (arrow) (O—O, trap No. 2;  $\Delta$ — $\Delta$ , trap No. 33; numbers, captures in each trap).

Habitat instability therefore makes estimates of the size of home range or territory at Cable Bay of doubtful value, particularly if they are obtained from pitfall data. Along with hand captures, pitfalls did, however, provide an indication of when the population moved as a result of structural change of the habitat. This in turn suggested the way in which the lizards were organised as a group in the long term.

Before May 1972 the *L. suteri* population was concentrated mainly within the quadrat, but individuals were found up to 60 m north of this area. A storm in May caused a large area of boulder beach, where lizards were previously abundant, to be scoured out of the centre of the quadrat, leaving only stones embedded in compacted sand. Sand was deposited on much of the area north of the quadrat, and a large log was stranded 5 m above HWL between traps 2 and 3, in an area not scoured by the storm. Pitfall and hand captures before and after this storm permitted reconstruction of the behaviour of the population over approximately 6 months.

Fig. 10 shows the numbers of lizards captured in trap 2 (near the log) as percentages of the total captured in the quadrat on trapping dates before and after the May storm. This is compared with catches in trap 33, which was in an area initially attractive to *L. suteri* but later deeply scoured by the storm. The increased proportion of captures in trap 2 after May can be attributed to movement of lizards from areas adversely affected by the storm into the more favourable area near the log. This movement across the quadrat towards trap 2 is demonstrated by plotting lizard captures before and after the May storm on to a map of the trap grid (Fig. 11). The decrease in captures at trap 2 (see Fig. 10) in September

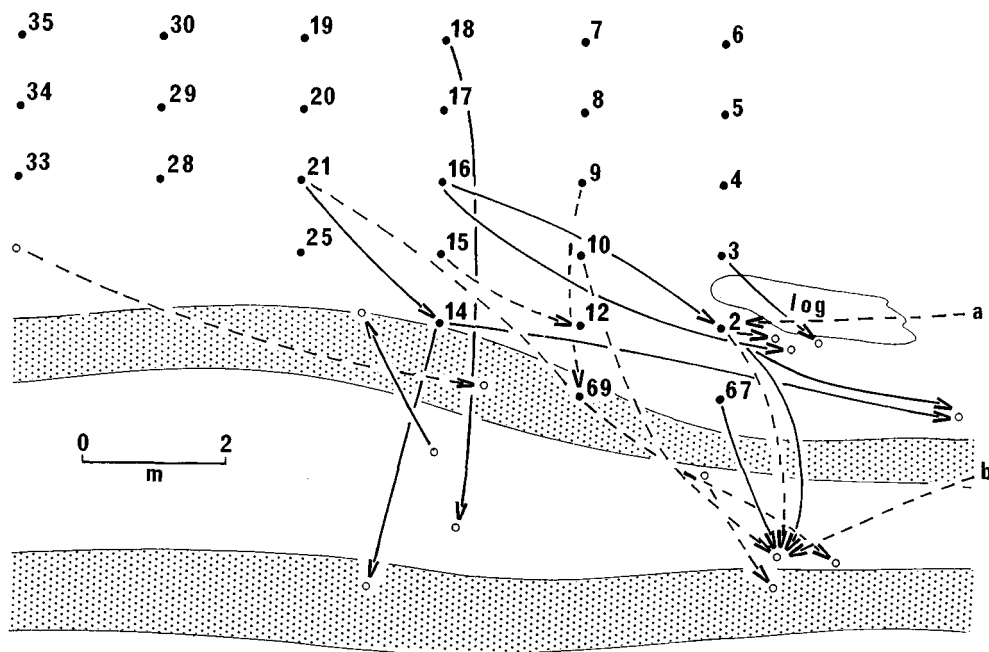


FIG. 11—Movement of juvenile (broken lines) and adult (solid lines) *Leiopisma suteri* before and after structural change of Cable Bay habitat, May 1972 (lines joining points do not necessarily represent path taken by lizard). Numbered dots, traps; shading, seaweed; a, b, movements of 33 m and 30 m from outlying traps.

and October is probably due to further movement. Several individuals captured at trap 2 (and those traps adjacent to it) between June and September were recaptured by hand in October near rotting seaweed (Fig. 11).

It therefore seems that trap 2 was situated in an area used as a winter refuge by the lizards disturbed by the May storm, some of which moved a few metres down the beach to feed near rotting seaweed in the warmer conditions of spring (September–November).

Twenty metres north of the quadrat, where lizards had been captured in pitfalls for over 12 months, the May storm deposited a large quantity of sand, smothering the lizards' habitat by filling the crevices between the stones. Skinks were rarely seen in this area until the last visit to the beach in October 1972 (Table 1).

The evidence for homesite preference in outdoor cages, the small amount of movement shown by adults, and the manner in which the population moved after the storm suggest that as long as suitable food and shelter are available at Cable Bay the lizards move little. However, when the habitat changes the population becomes reorganised, and within each situation a dominance hierarchy may exist, at least for males. These same principles also appear to apply to the juveniles and hatchlings, except for aggressive behaviour, which seems to be restricted to adult males. The concentration of hatchlings in marginal habitat means that adverse factors affecting the adults influence this group first.

#### SURVIVORSHIP

Hatchlings ( $n = 63$ ) were the least abundant age class (juveniles,  $n = 83$ ; adults,  $n = 125$ ) in pitfall and hand catches over the period in which these were obtained simultaneously (April–October 1972), although from casual field observations they appeared to be the most common group. This was due to the difficulty of capturing these small lizards amongst the

Trapping period	Lizards captured	Traps set
Dec 1971	15	18
Jan 1972	5	18
Feb	12	18
Mar	4	18
Apr	5	18
<hr/>		
Jul	1	10
Aug	—	10
Sep	1	13
Oct	—	13

TABLE 1—Captures of *Leiopisma suteri* north of Cable Bay quadrat before and after May 1972 storm, when most of the pitfall traps were buried and not found until July (—, nil)

TABLE 2—Proportion of recaptures of each age class of *Leiopisma suteri* from Cable Bay, from all lizards marked and recaptured over 19 months (—, nil)

No. marked as:	Recaptured as:	Marked animals/age class recaptured (%)
Hatchlings 59	Hatchlings 3	5.1
	Juveniles 2	3.4
	Sub-adults —	—
	Adults —	8.5
Juveniles 129	Juveniles 10	7.8
	Sub-adults 1	0.8
	Adults 8	6.2
Sub-adults 9	Sub-adults 1	11.1
	Adults —	—
Adults 145	Adults 45	31.0

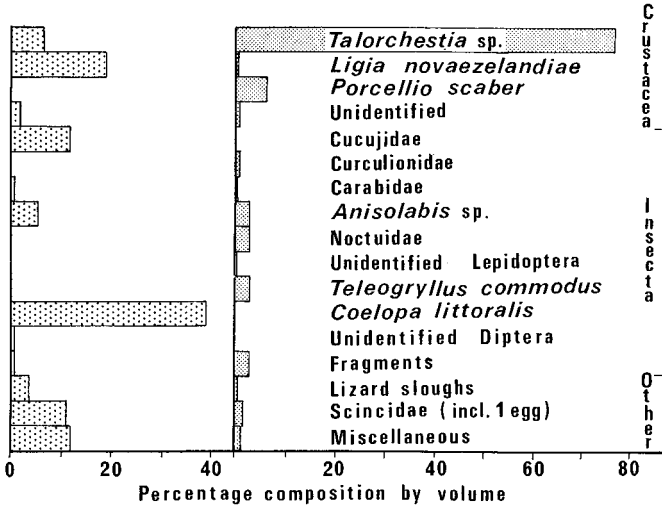


FIG. 12—Percentage volume composition of stomach contents of *Leiopisma suteri*: stipple - outside Hauraki Gulf, including islands from Poor Knights to Mercury group (n = 32); shading - inner Hauraki Gulf, including Motutapu I. (n = 48), Waiheke I. (n = 3), and Rangitoto I. (n = 5).

boulders by hand, rather than to a demographic curve skewed towards the adults. It was therefore not possible to construct life tables for *L. suteri* at Cable Bay. However, an indication of relative survivorship of the age classes was obtained by comparing the chances of recapturing marked individuals from each (Table 2). The low percentage of hatchlings and juveniles recaptured in comparison with adults appears to be an approximate measure of mortality rather than emigration, because Cable Bay was isolated from any other population of the same species.

## FEEDING

## POTENTIAL PREY

Attempts were made to quantify seasonal changes in the composition of potential food organisms of *L. suteri* at Cable Bay, but these proved to be unsatisfactory and were abandoned. Instead, changes in relative abundance of the common arthropod groups were estimated.

Groups abundant in summer included *Teleogryllus commodus*, Noctuidae, *Anisolabis* sp. young (adults were common throughout the year), and *Porcellio scaber*. *Talorchestia* sp. was abundant for most of the year, although dried seaweed did not support many in summer. In winter, the abundance of *Talorchestia* increased with deposition of fresh seaweed and then appeared to decrease as the seaweed became soaked with rainwater. The littoral isopod *Ligia novaeseelandiae* was present only under recently deposited seaweed. Adults of the earwig *Anisolabis* sp., which were about 30 mm long, were too large to be taken regularly, but young earwigs, which were most numerous in spring and summer, were within the size range of potential prey animals. Usually the most important food items were abundant only when there was a large supply of seaweed.

## STOMACH CONTENTS

Feeding habits may be elucidated by several methods, including examination of scats (Lewis 1951) and stomach and intestinal contents. Scats and intestinal food remains of *L. suteri* tended to be fragmentary, but stomach contents were often entire and easily identified, and were accordingly examined in detail. The stomach contents examined were from adults only, to allow comparison with lizards (Ecology Division, DSIR, collection; mostly adults) from outside the Motutapu Island area (Fig. 12). These show that, as for the other New Zealand skinks so far studied, the range of prey taken is wide, though several items which appeared only once or twice cannot be considered typical.

The bulk of the stomach contents from Motutapu *L. suteri* consisted of *Talorchestia*, isopods, and *Anisolabis*. Most of the isopods were the terrestrial slater *Porcellio scaber*, taken by lizards foraging in the doab; in contrast, the lizards from other islands were more commonly found to contain *Ligia novaeseelandiae*. Fragments of adult *Anisolabis* appeared occasionally, and could be recognised by the large anal pincers, but young ones were more common in the stomach contents. Noctuid moths were preyed on as both larvae and adults, and appeared in lizards collected in April and June 1971. These are probably only a seasonal food, again available only to lizards foraging in the doab grass. Of interest was the presence of a lizard egg in the stomach of a specimen of *L. suteri* collected in late December at Cable Bay.

The stomach contents of *L. suteri* from outside the Motutapu Island region covered a similar range of food items, but differed in the proportions of each food type. Large, white maggots and brown pupae, probably of the kelp fly (*Coelopa littoralis*), dominated the food items identified from lizards collected in the Hen and Chickens Islands; the stomach of one lizard from this group contained 21 maggots and 2 pupae. Adults of these large kelp flies were not found in any of the lizards examined, and neither larvae nor adults were found in individuals from Motutapu.

"Miscellaneous" remains consisted mainly of vegetable matter. This was present infrequently, and at least some of it was probably ingested accidentally when catching moving prey.

The stomachs of two lizards captured on a stack in the Hen and Chickens group contained the remains of the tails (green) of unidentified skinks. This need not indicate that *L. suteri* are active predators of other lizards; the tails may already have been shed.

	Mean volume (% of standard)	Range (%)	n
Apr 1971	28.8	3-53	4
May	1.2	0-3	5
Jun	2.6	0-9	5
Jul	1.6	0-8	5
Aug	7.3	0-12	3
Nov	59.0	17-94	4
Dec	21.0	3-57	4
Jan 1972	3.8	0-6	4
Feb	12.3	0-30	4
Mar	36.5	21-47	4
Apr	47.5	28-75	4
Aug	4.0	0-12	3
Sep	93.0	28-194*	5
Oct	59.3	12-147*	4

TABLE 3—Mean monthly volume of stomach contents of *Leiopisma suteri* from Cable Bay

\*Filled to a greater volume than the standard (see Methods)

#### FOOD SOURCES

In addition to stomach content analyses, *L. suteri* prey was macroscopically identified by examining scats. Except in wet weather, these were found on stones at Cable Bay in the area where lizards were common. Around rotting seaweed the faecal pellets were predominantly of *Talorchestia* remains, which gave them a brick-red colour, whereas under doab grass the pellets were generally black, being composed of insect fragments. Faecal pellets and stomach contents reflected a diet of the most common arthropods in the area in which the lizard was captured, suggesting that *L. suteri* at Cable Bay does not forage widely. The most favoured food source area is near seaweed jetsam, with which most of the food items taken by *L. suteri* (86.3% of identified remains at Motutapu and 94.7% outside this region) are directly associated, viz. *Talorchestia*, *Ligia*, kelp fly maggots, and *Anisolabis*.

#### SEASONAL CHANGES IN STOMACH VOLUME

When *L. suteri* has not fed for some time the stomach lining becomes thick and strongly ridged, in contrast with the thin-walled, distended stomach of repletion. On Motutapu Island, skinks with empty stomachs were found on several occasions (Table 3). Although the sample sizes are small, it is evident that stomach volumes tended to be largest in autumn (until April) and spring to early summer (September–December), and smallest in midsummer (January) and during the hibernation period (May–August). Low midsummer stomach volumes coincided with a shortage of seaweed at Cable Bay (see Fig. 4). Where food was available the volumes measured were variable, and where food was in short supply, or lizard activity was limited, the volumes recorded were consistently low.

The lizards with thick-walled stomachs from May to August were found at a time when amphipods were abundant. Reduction in stomach content volume during winter can therefore be attributed to reduced activity at low temperatures, rather than lack of food.

#### HIBERNATION (BRUMATION)

Mayhew (1965) has proposed that the winter inactivity of ectothermic vertebrates be described as 'brumation, to avoid confusion with studies of endotherms. However, the term 'hibernation' has been used in most recent reptile studies (e.g., Tinkle 1967; Bustard 1968a, b, 1970, 1971; Platt 1969; Bellairs 1969; Telford 1969, 1970; Goldberg 1972), and I therefore adopt it to describe the winter inactivity of *L. suteri*.

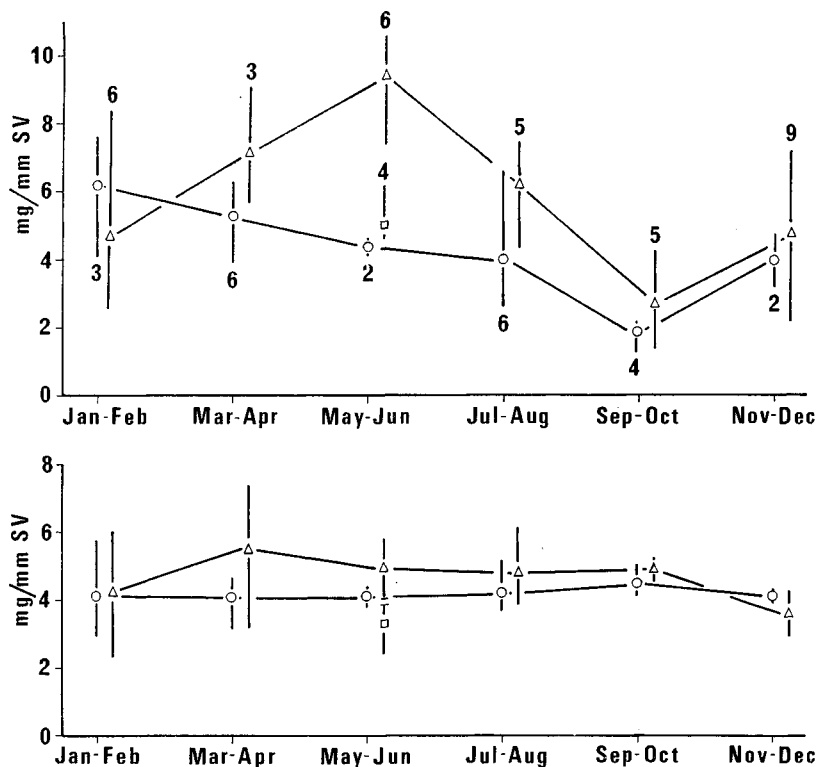


FIG. 13—Fat body weights (a) and liver weights (b) of *Leiolopisma suteri* (△, ♀♀ and ○, ♂♂ from Cable Bay; □, ♀♀ from Cuvier; vertical lines, range; numbers, sample size (samples summed into 2-monthly groups); measurements, weight as a fraction of snout-to-vent length).

The extent to which lizard activity is limited by winter conditions can often be assessed from the size of the main lipid storage tissues, i.e., the inguinal fat bodies and the liver (Goldberg 1972). These are also used by reptiles during development of reproductive tissues, so the two processes may draw upon nutrient stores simultaneously. The fat body sizes of *L. suteri* from Cable Bay decreased throughout the winter (Fig. 13a), over which period adults were rarely encountered in the field. Fat bodies from females showed a more marked seasonal change than those from males, indicating that these organs supply nutrients towards vitellogenesis. Liver weights, however, showed no obvious seasonal change for either sex, although the livers of females were larger than those of males for most of the year (Fig. 13b). Fat bodies and livers of four adults from Cuvier Island were compared with those from Cable Bay individuals collected at the same time of year. Both organs were larger in the Cable Bay specimens, raising the possibility that nutrient reserve changes do not occur in a similar manner throughout the lizards' range.

The lack of obvious change in liver size of *L. suteri* suggests that the fat bodies provide adequate nutrient reserves for reproduction and hibernation, and implies in turn that activity is not completely curtailed during winter, the lizards probably emerging occasionally during warmer conditions to feed. Fat bodies of female *Leiolopisma zelandicum* vary greatly in size at different times of the year, immediate post- or pre-parturition females often entirely lacking these organs (Barwick 1959). This indicates that the fat reserves of *L.*



TABLE 4—Numbers of *Leiopismis suteri* captured in transects at Cable Bay, October 1972 (—, nil)

	Hatchlings	Juveniles	Adults		Area sampled (m <sup>2</sup> )	No./m <sup>2</sup>
Transect 1	7	1	—	8	2.3	3.5
„ 2	27	28	17	72	2.8	25.7
„ 3	11	1	12	24	3.2	7.5
	45	30	29	104	8.1	12.6

*zelandicum* are more heavily utilised than those of *L. suteri*, though neither species undergoes complete hibernation. The difference might be due partly to different forms of reproduction, *L. suteri* being oviparous and *L. zelandicum* viviparous. The drain upon food reserves during development of young lizards or eggs is usually greater for viviparous than for oviparous species (Fitch 1970).

Recent work has shown that fat stores in the body wall and tail are important nutrient reserves (Clark 1971, Gaffney & Fitzpatrick 1973, Smyth 1974). This is probably true also for *L. suteri*, since tails of individuals kept without food become noticeably emaciated.

#### DISCUSSION

Except for marine iguanas, most of the references to lizards inhabiting the coastal fringe relate to Scincidae (Mertens 1960, Alcalá & Brown 1967, Fricke 1970, Cogger 1971). In New Zealand, several skink and gecko species may at times inhabit the area close to the shoreline (Whitaker 1968b, Towns 1972), although in most instances this is only one of a number of habitats in which the species may be found. *L. suteri* is the only species with a range restricted to the upper shoreline. On islands where Polynesian rats do not occur, *L. suteri* is found on rock platforms and shingle beaches, foraging at night in the open (Whitaker 1973). Where rats are present these skinks are usually found only on boulder beaches, and they are apparently active only beneath the beach surface. Predation pressure is not, however, the only reason for the presence of *L. suteri* on boulder beaches; populations also occur in this habitat on some islands of The Aldermen group, where rats are absent (Towns & Hayward 1973, Whitaker 1973).

Boulder beaches of the type inhabited by *L. suteri* tend to be formed on moderately open coasts, and are especially common on offshore islands (Morton & Miller 1968). For the beaches to be suitable for *L. suteri*, it appears that a steady supply of storm-tossed seaweed is necessary. This usually occurs with moderate exposure, and possibly with proximity to offshore currents in which detached weed is carried. In addition, the beaches must provide stable areas in which lizards are protected during storms. The optimum combination of exposure and stability may not occur on all beaches of a particular island, as appears to be the situation on Lady Alice Island (Hen and Chickens group), where *L. suteri* is found on one small beach from a total of four. Similarly, on Red Mercury Island the species is present only in one small cove, although the island is almost encircled by boulder beaches.

Because the beach at Cable Bay showed the effects of disturbance for long periods, an attempt was made to estimate the size of the lizard population without disturbing the habitat. Fourteen months' capture/recapture data were obtained using pitfall traps set on a grid (the relative merits of grid and random trapping are discussed by Eberhardt (1969)). However, it was subsequently found impossible to obtain an unbiased population estimate from standard capture/recapture methods (although 342 lizards had been marked), for the following reasons. First, pitfall captures were biased away from hatchlings and towards the

adults because the traps could be placed only in more stable parts of the beach. Second, if the adults were considered in isolation, the number of recaptures was too small for Jolly-Seber estimates (Seber 1973). Third, births into the population and disturbance of the habitat by storms made it impossible to isolate a constant population from which a Petersen estimate could be calculated.

Pitfall captures might have been more successful if intensive trapping had been carried out for short periods, but there would still have been bias towards the adults, and there would also have been difficulties in comparing summer with winter results. Generally very few adults were captured during winter, because lower temperatures suppressed activity.

The alternative to pitfall trapping was estimation of population size from direct observations of density. Lizards were captured along three belt transects, covering 8.1 m<sup>2</sup> (5.4% of the total area inhabited by *L. suteri*) within a 0.25 × 0.25-m iron enclosure with 20-cm-high sides. The enclosure was placed amongst the stones, which ranged in depth from 2 cm to 18 cm (mean, 8.4 cm; no. of measurements, 29), and all the lizards within it were captured. For logistic reasons the three transects were placed non-randomly (see Fig. 2), where lizards were known to be present. Consequently the figures are only an index of density over the optimum habitat, rather than a mean for the whole study area.

The three transects gave an average density of 13 *L. suteri* per m<sup>2</sup>, but there are wide fluctuations in the figures over short distances (Table 4). At one site, where the skinks were congregating near rotting seaweed which supported large numbers of littoral amphipods, 36 lizards were captured in the enclosure (equivalent to 144/m<sup>2</sup>). Biomass was calculated from the density estimate using the following mean weights of *L. suteri* at Cable Bay: hatchlings, 2 g; juveniles, 4.5 g; adults, 8.5 g. Using the age-class composition of the lizards captured in three transects, a mean biomass of 65.4 g/m<sup>2</sup> (654 kg/ha) was obtained. *L. suteri* populations on boulder beaches tend to be highly clumped, so a biomass in terms of kg/ha is rather unrealistic. Even so, these figures are far higher than those of Ruibal & Philibosian (1974) for the arboreal lizard *Anolis acutus*, which at one site had a mean density of up to 0.43 lizards/m<sup>2</sup> and a biomass of 13–23 kg/ha — one of the highest lizard densities previously recorded. The high densities reached by *L. suteri* on boulder beaches are probably due partly to the structure of the habitat, which in favourable areas enables the population to form several strata compressed into a few centimetres. A similar situation would occur with arboreal species, but the strata would be more widely spaced. These three-dimensional habitats therefore have a higher potential carrying capacity than the two-dimensional habitats, such as wasteland, more commonly described in the literature (see References in Tinkle 1967). Whitaker's (1968b) estimate of 600–650 *L. suteri*/acre (recalculated as 0.07–0.09 lizards/m<sup>2</sup>) for a rock platform population is far lower than the 13/m<sup>2</sup> estimated from this study for a boulder beach population, demonstrating the effect on homesite availability of increased habitat complexity.

Rock platform populations of *L. suteri* probably resemble wasteland lizard populations in having reasonably stable temporal and spatial boundaries. In comparison, boulder beach populations appear to have unstable boundaries, at least spatially, as a result of movement out of areas which have become unfavourable because of habitat disturbance.

Habitat instability seems to be a major factor limiting the size of the *L. suteri* population at Cable Bay. During the 19-month study period, storms were severe enough to wash over the entire lizard habitat on at least three occasions. Individuals congregated near high water at such times would be the first to suffer from disturbances, so there is probably a high mortality amongst hatchlings in this area, as indicated by the low recapture rate for this age class. Since hatchlings tend to be the most common group in marginal habitat, they will

also bear the brunt of such biotic factors as food shortages and predation, and physical influences (other than habitat change) such as high summer temperatures and low winter temperatures. Food shortages occur occasionally in the high tide region; Cable Bay, for instance, was practically bare of seaweed from August 1971 until April 1972. Under these conditions adults can feed on terrestrial invertebrates towards the back of the beach, but most of the hatchlings appear to remain near high tide level.

The tendency for hatchlings to be most common in the least stable areas of a beach implies movement of several metres from the hatching site, since the few *L. suteri* nests which have been found were all in the most stable parts of boulder beaches (Whitaker 1968a). This movement may result from the agonistic behaviour of adults, or from attraction to areas where newly deposited seaweed provides abundant food, or, as seems most likely, the two in combination.

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