CHAPTER 7

ECOLOGY

HOME RANGE, MOVEMENT AND BEHAVIOUR

The previous chapters have all dealt with aspects of the life cycles of various reptiles and amphibians on the Nylsvley Nature Reserve. It was possible through observation and mark-recapture sampling to collect data on their home range size, movement and behaviour, during the two-year period of the study. While extensive movement by amphibians has been mentioned in the previous chapter, and is important to ensure breeding, large scale movements of the reptiles, particularly snakes, are not well documented. Movement consists basically of three types involved with food seeking, reproduction and exploration. At certain times of the year one activity may merge into the other, but each type has certain characteristic behaviour. There are only two territorial reptile species at Nylsvley while several species, notably lizards, possess definite home ranges. As the size of home ranges is dependant on frequency of sighting or capture, the data obtained pertains specifically to those species which occur in greater numbers.

Snakes

Although a large number of snakes was captured during the two-year period, it was only possible to determine home range size for a single species, namely the vine snake (Thelotornis capensis). The vine snake is a unique species, being totally arboreal and exhibits a behaviour unlike that of other reptiles. Vine snakes are diurnal reptiles with acute sight and the widest binocular fields of vision known for any snake, Henderson & Binder (1981). In the Study Area a total of 147 vine snakes was captured over the period May 1975 to December 1977. Of these, 78 have been recaptured or re-sighted on at least one occasion, but some were found on five or more occasions. September 1975 provided the first indication of unusual behaviour. During the trapping period, a total of 18 snakes was found scattered in the south-east corner of the Study Area, mostly (78%) occupying Grewia flavescens shrubs. This aggregation was also seen during 1976 and 1977, where 12 and 15 vine snakes respectively, were found under similar conditions. Several were together copulating and sometimes three were found in the same bush. This predilection for Grewia flavescens shrubs is a marked feature of this snake during spring and early summer (Figure 85 and Table 46).

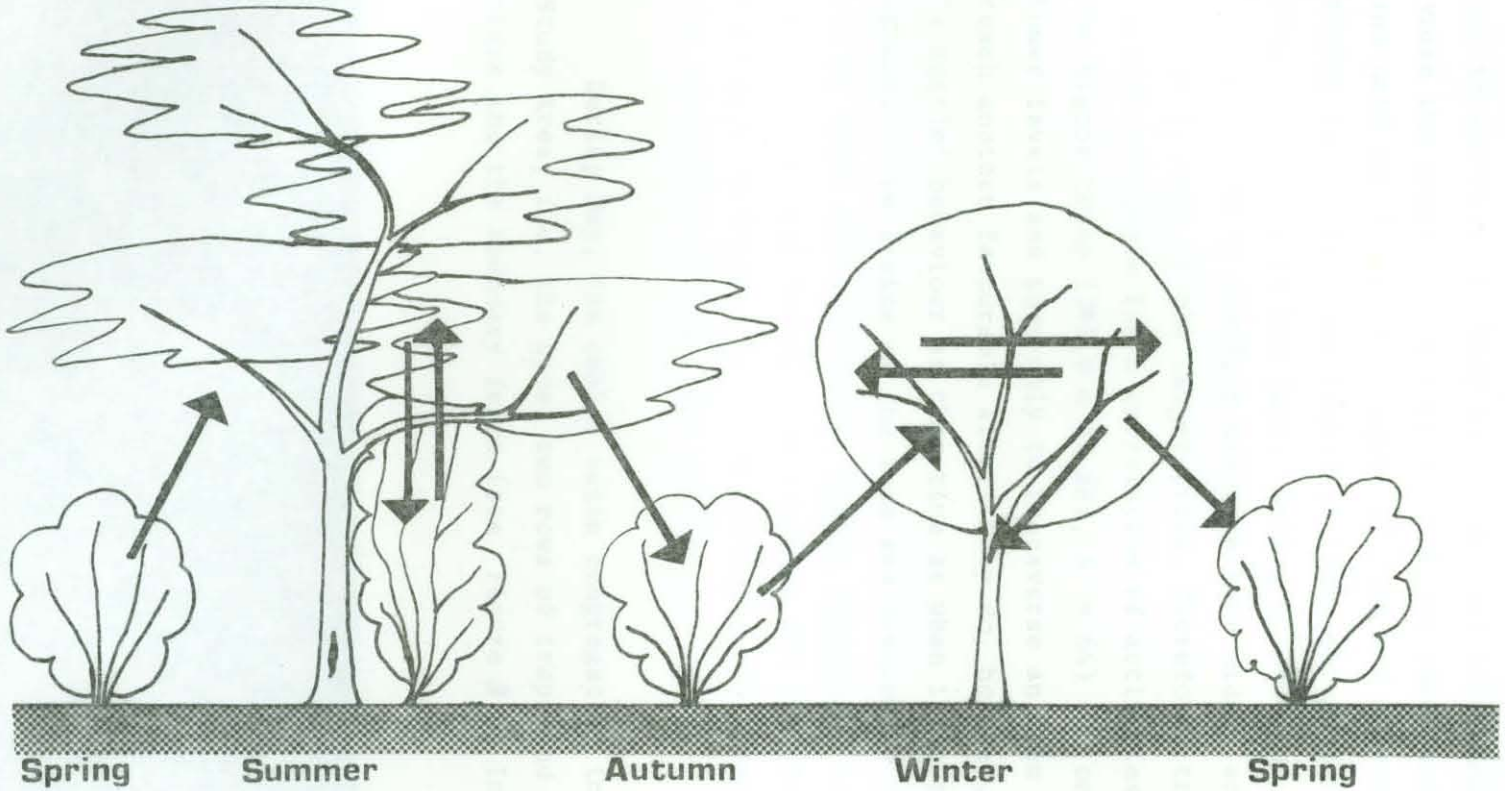


Figure 85. A schematic representation of seasonal movement of Thelotornis capensis in the Burkea africana - Eragrostis pallens Study Area.

Table 46. Seasonal tree species selection by Thelotornis capensis in the Burkea africana - Eragrostis pallens Study Area : May 1975 - May 1977, expressed as a percentage for each month.

Tree Species	J	F	M	A	M	J	J	A	S	O	N	D
Grewia flavescens	66,7	100	77,8	75,0	41,9	3,7	10,0	21,9	72,5	62,5	62,5	41,7
Strychnos pungens	0	0	0	0	9,7	72,84	65,0	32,9	5,9	0	0	0
Others	33,3	0	22,2	25,0	48,4	23,5	25,0	45,2	21,6	37,5	37,5	58,3

The snakes chose on average low positions in these shrubs (75,4% <1,5 m, N = 51) and may be found in a variety of positions but normally with the body and head outstretched within the shrub. Occasionally they would be seen with the fore-quarter or third of the body protruding rigidly from the bush. On being approached, all movement is followed by tilting the head so as to keep the approacher in view.

They rely to such a degree on their camouflage ability that they allow one to encircle the body with thumb and fore-finger without moving, provided the snake is not touched. At the same time, the tongue is protruded and held out for short lengths of time and movement in and out is very slow. During summer they may remain in these shrubs for relatively short periods, occasionally up to two days. During October and November and then on until March, these reptiles disperse more widely and are difficult to find in the foliage of the larger trees. Therefore, there are relatively few records available for a correlation of activities. However, they take to the higher trees (>2,0 m 21,88%, N = 64) and only rarely descend to the lower levels and then only to transverse an open piece of ground and so reach another favourable site. They do, however, exhibit a type of 's huttle' behaviour at this time as when it is hot they descend from the canopy to the inside of the tree and frequently into shrubs below the canopy where there is shade. Grewia flavescens is frequently found scrambling up into the larger tree canopies and the snakes are often found under such circumstances. This, therefore, is responsible for the high ratings for this shrub during these months.

During May, the snakes begin congregating in the upper portion of the Study Area, i.e. the upper two rows of traps and that section between these traps and the boundary fence (see Figure 3). In contrast to September,

they move into Strychnos pungens trees with its sharp-tipped, virtually evergreen foliage. Here most spend the winter, although when it is particularly cold, they enter holes in trees and hibernate under these conditions. Many, however, remain outside virtually throughout the winter and may be found day after day in the same tree or group of trees, some specimens remaining for up to three months in the same tree. Many do not truly hibernate as they exhibit diurnal movement, moving out onto the extended branches of the tree to bask on the east side in the morning, returning possibly to the centre during the middle of the day, and out on the west side in the afternoon. Others disappear during July and actually may enter holes in trees even at soil level and hibernate as they do not emerge until spring. This then is the typical scene during the winter months. They therefore have, in effect, seasonal home ranges, which in winter may only be the perimeter of the foliage of the tree or trees and, therefore, only measures several square metres in extent.

However, their summer ranges are far more extensive and vary from about five to eleven hectares. In some instances, individuals make exploratory moves extending 300 m or more from their normal haunts. However, they do return in due course. Size of home ranges was delimited by a line mid-way between the sighting and the next series of traps, i.e. an extra 50 m all round. Only those snakes with five or more sightings were included in these calculations. The average home range size was 4,6 ha n = 19 (Figure 86) and a considerable overlapping was found. The distribution of these snakes within the Study Area can be seen in Figure 87 using frequency of occurrence at the various trapping sites. It will be remembered that observations on these snakes are based on sightings and not captures in traps. It will be noticed that there is a centre of abundance in the upper part of the Study Area which appears to be particularly favourable to the vine snakes with a larger surrounding area where vine snakes were also found to be relatively abundant. The distribution appears largely to be correlated with the density of shrubs and trees in this portion of the Study Area.

Further to the west, along the downslope towards the turf vlei, the trees open up and a denser grass cover is found, while Grewia flavescens and Strychnos pungens become far fewer and in the case of the latter almost non-existant. There are possibly two reasons for this anomaly. One is that lower down the slope the cold intensifies although the slope is

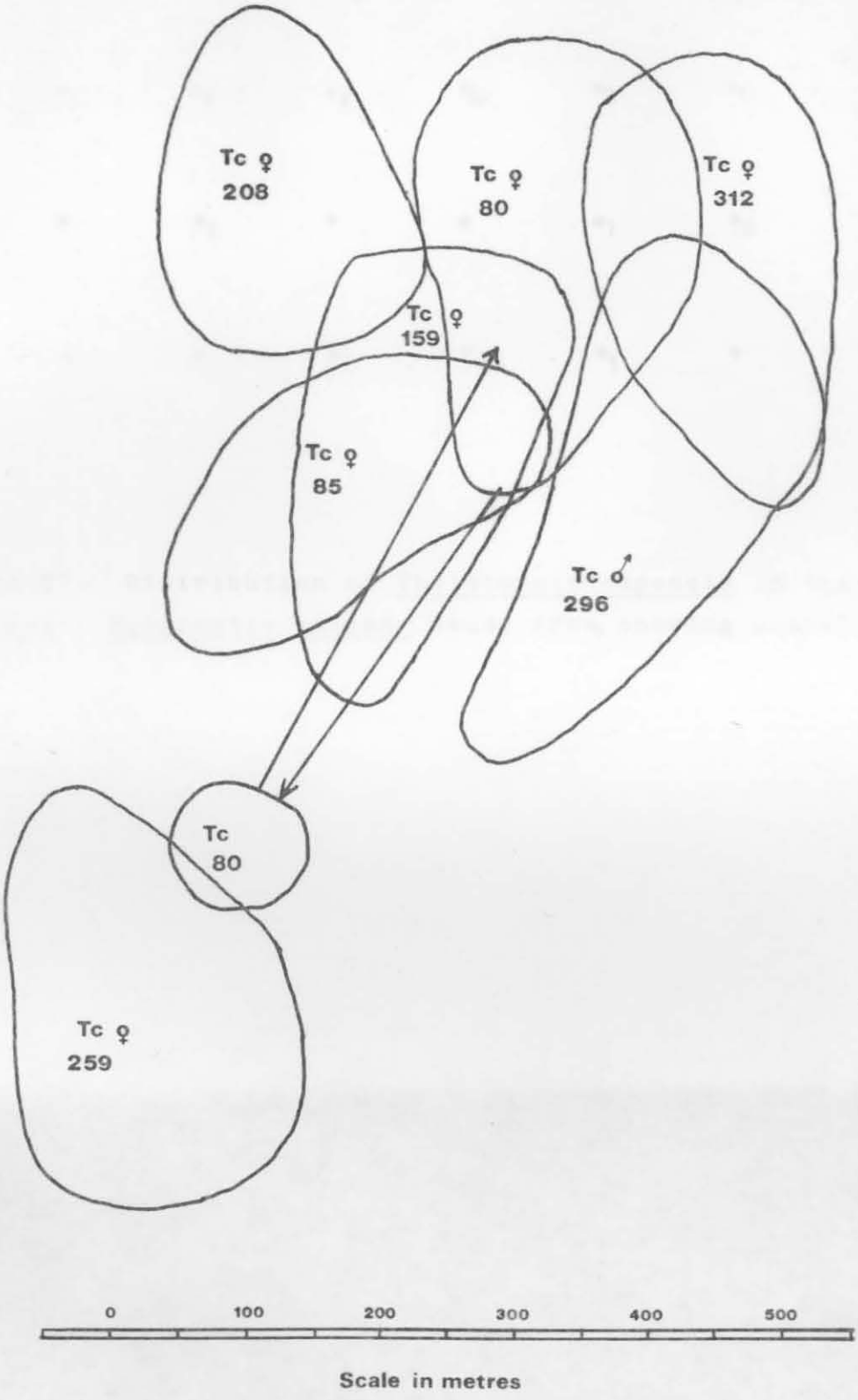


Figure 86. Home ranges of Thelotornis capensis in the Study Area.

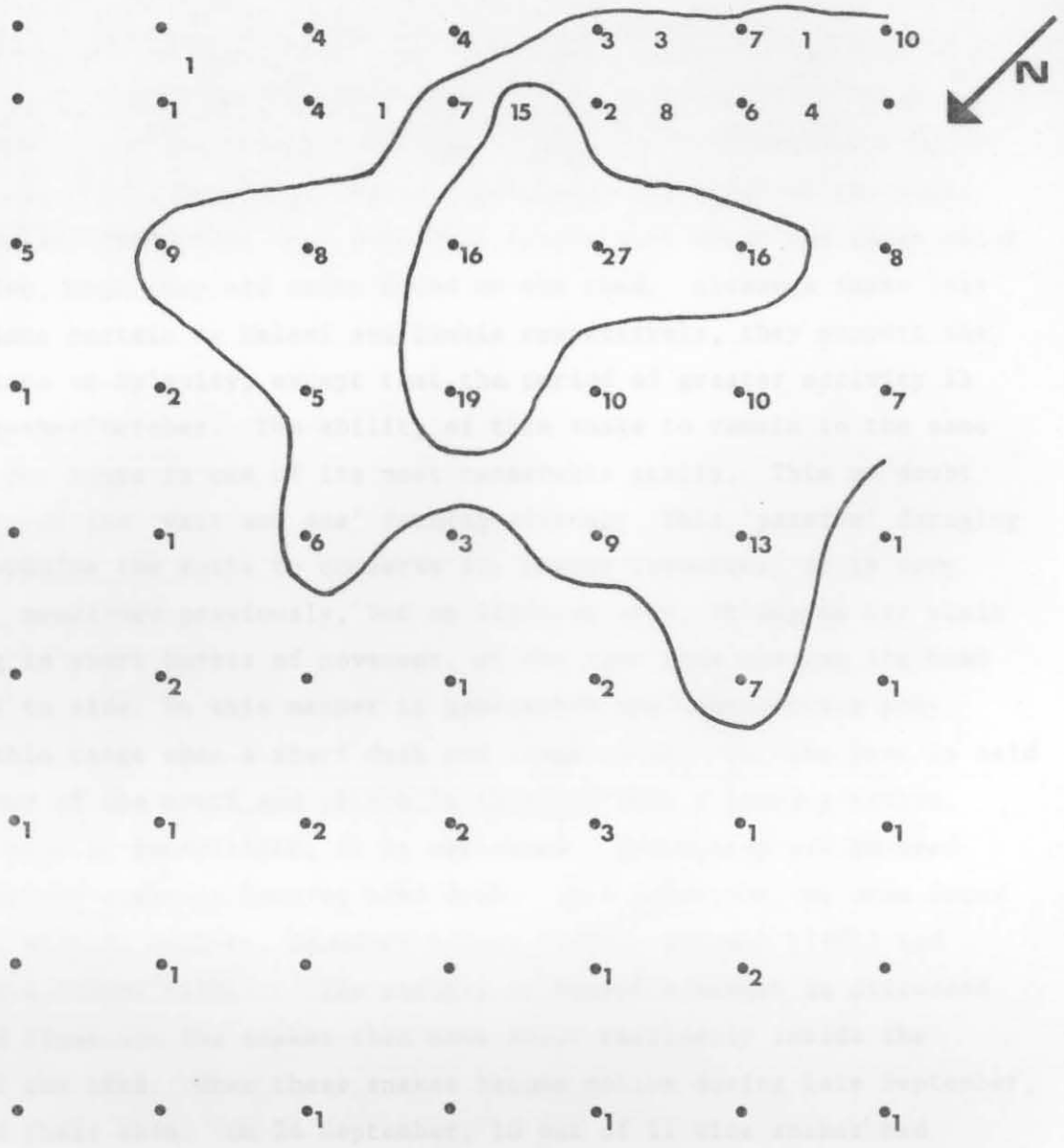


Figure 87. Distribution of Thelotornis capensis in the Burkea africana - Eragrostis pallens Study Area, showing anomalies.

very gradual, or secondly, the impeded drainage affects the growth of the two woody species which feature so prominently in the life style of this snake in the Study Area.

It is, however, probable that the small temperature differences as well as the fact that Strychnos pungens is evergreen during winter are responsible for the movement of these snakes to the top end of the Study Area. Extensive searches, both below and outside the Study Area reveal that this is definitely a preferred site. Figure 88 shows the distribution of these snakes according to sightings and capture over 3-month periods. It is clearly discernible how the pattern changes from highly localised during autumn and winter, to being widespread during spring and summer.

Sweeney (1971), also found that vine snakes remain in one area for several days and may 'wander' in a limited area on a number of trees. He concluded that the occurrence of Thelotornis was dependent on climatic conditions and that they were rare at seasonally dry times of the year. Wilson (1965), found that they were most active just after the first rains have fallen, when they are often found on the road. Although these last observations pertain to Malawi and Zambia respectively, they support the observations on Nylsvley, except that the period of greater activity is late September/October. The ability of this snake to remain in the same position for hours is one of its most remarkable traits. This no doubt forms part of its 'wait and see' feeding strategy. This 'passive' foraging pattern enables the snake to conserve its energy resources. It is very alert as mentioned previously, but on sighting prey, it begins its stalk by moving in short bursts of movement, at the same time swaying its head from side to side. In this manner it approaches the unsuspecting prey, until within range when a short dash and lunge secures it. The prey is held in the rear of the mouth and poison is injected with a chewing action. Once the prey is immobilized, it is swallowed. Swallowing can proceed even while the snake is hanging head down. This behaviour has been documented by several authors, Broadley & Cock (1975), Sweeney (1971) and Henderson & Binder (1981). The ability to remain extended is disturbed when wind blows and the snakes then move about restlessly inside the canopy of the tree. When these snakes become active during late September, most shed their skin. On 26 September, 10 out of 11 vine snakes had sloughed. Sloughing is not correlated with growth per se, but appears to be an irregularly timed mechanism of removing dead skin layers.

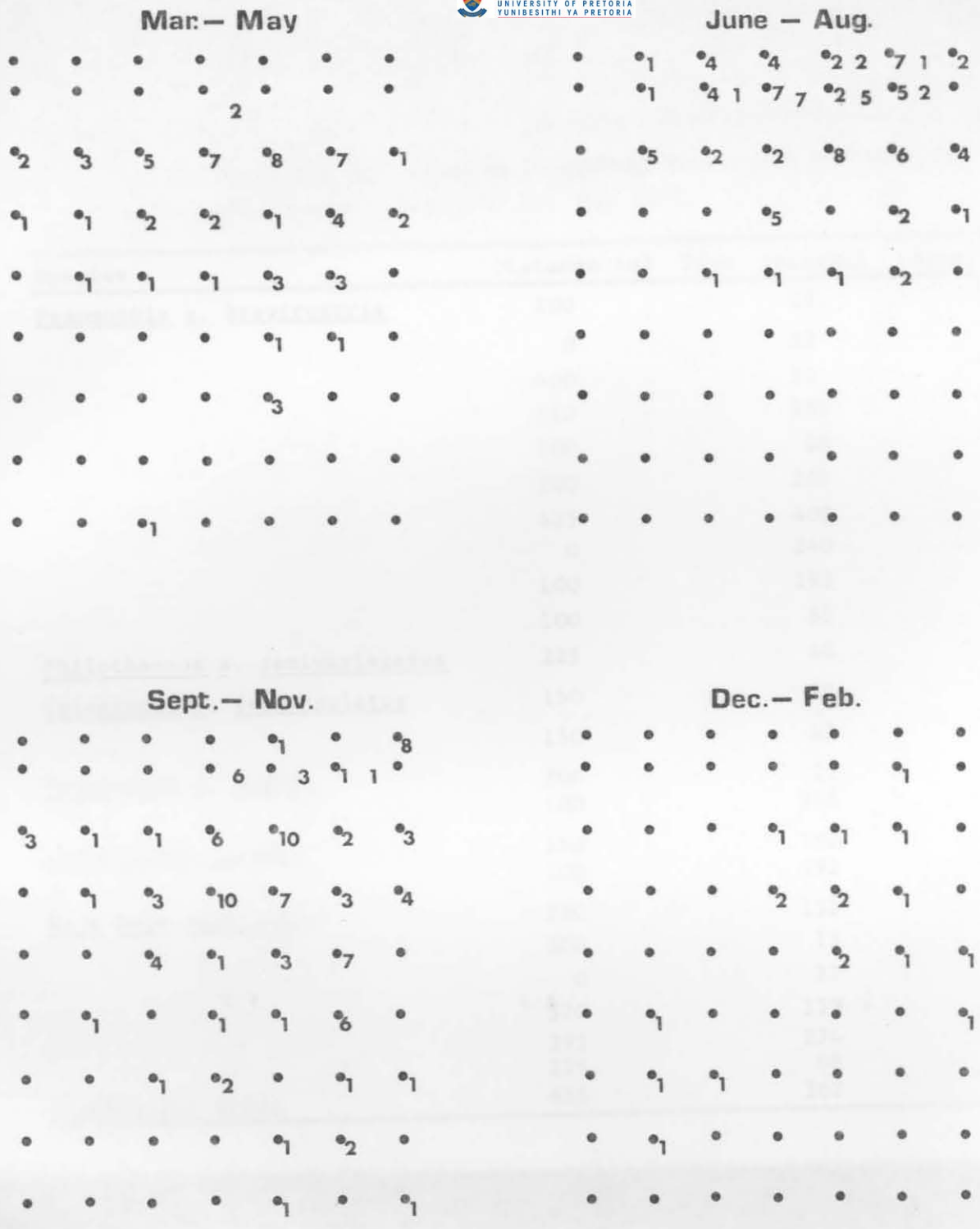


Figure 88. Seasonal variation in the distribution of Thelotornis capensis in the Study Area.

In contrast to the 'percher' attitude of the vine snake, the other species actively forage. This is particularly so of the short-snouted sand snake (Psammophis s. brevirostris), which is an active diurnal snake. It moves about slowly while foraging, but if prey is sighted, it follows with an accellerated dash, catching its prey. It is extremely agile and the head follows each movement of the prey. The prey is also held until dead or immobilised after which it is swallowed, usually head first. These snakes do not appear to have home ranges, as they disappear for long periods, only to reappear in traps 100 m from where they were originally trapped. A total of 82 individuals were captured, of which 12 were recaptured on single occasions. As the times of capture/recapture were widely separated, it is therefore only possible to present the distances between these times, as the shortest route between the points. This is actually applicable to all the species (Table 47).

Table 47. Distances between sites of capture and recapture of snakes in the Burkea africana - Eragrostis pallens savanna on the Nylsvley Nature Reserve : May 1975 to May 1977.

Species	Distance (m)	Time interval (days)
Psammophis s. brevirostris	200	29
	0	32
	400	20
	510	189
	100	28
	100	207
	635	409
	0	240
	100	293
	100	85
Philothamnus s. semivariegatus	225	46
Telescopus s. semiannulatus	150	32
	150	47
Dasypeltis s. scabra	200	21
	100	346
Lycophidion capense	150	150
	200	192
Naja haje annulifera	200	131
	500	13
	0	77
	320	355
	395	274
	225	88
Dispholidus typus	655	362

Species	Distance (m)	Time interval (days)
Crotaphopeltis h. hotamboeia	100	37
	100	30
	150	219

It is apparent that the results are highly variable, with indications and contraindications of a home range. It was previously discussed that some American snakes, such as the Racers which have similar habits, have extended 'home ranges' up to 700 m in diameter, which may indicate a similar situation among the sandsnakes. However, it does not explain why 85% of the short-snouted sandsnakes captured were never seen again. Similar arguments can be made for the other species with equally poor recapture results, but when recaptured are only short distances from the site of original capture. The only other snake species recaptured which travels over long distances is the Egyptian cobra (Naja haje annulifera) but this is to be expected as the larger species need a greater foraging range in which to locate prey.

Therefore, although there are indications of possible home ranges, these are in effect largely obscured by the great turnover of these snakes during the trapping period. It is illogical to assume that most snakes become trap-shy after their initial capture, but it is difficult to account for this trend.

Lizards

Almost as varied as the snakes, the lizards are represented by species with similar foraging strategies as those of the snakes. The most active forager is the Cape rough-scaled lizard (Ichnotropis capensis) which moves about actively foraging, often in short bursts of movement followed by a slower cursorial inspection of an area. If prey such as a grasshopper is disturbed and bounds away, the lizard will follow very rapidly. Similarly, during its search for termites and spiders, it digs and scrapes among the leaves often quite vigorously. They course the area extensively and from recaptures it was possible to ascertain the extent of their home range. The mean home range size is 622,5 square metres (n = 12). No agonistic behaviour was observed and in fact few interactions occurred, although home ranges overlapped (Figure 89). When two lizards met they touched each other with their tongues, after which they parted and continued foraging.

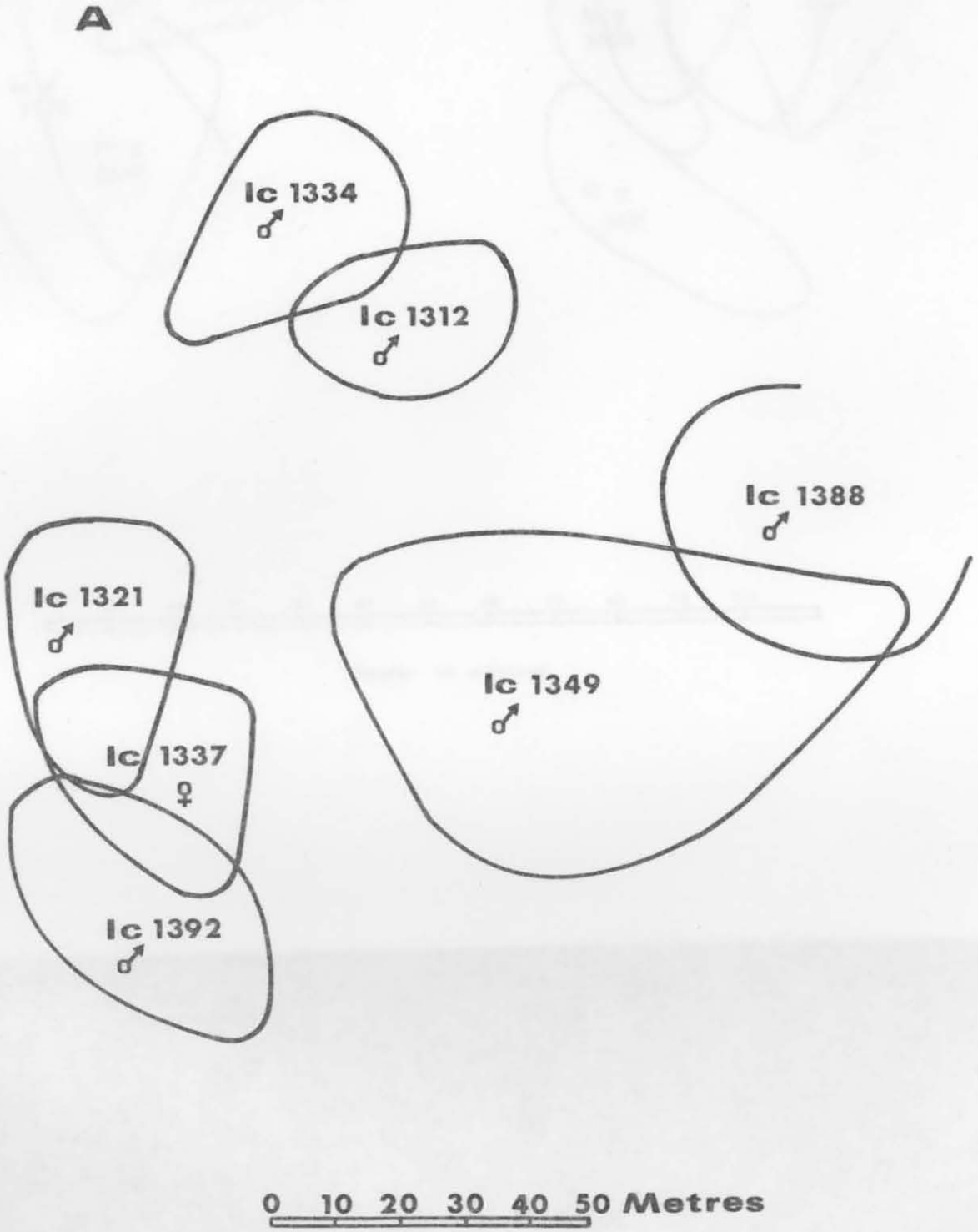
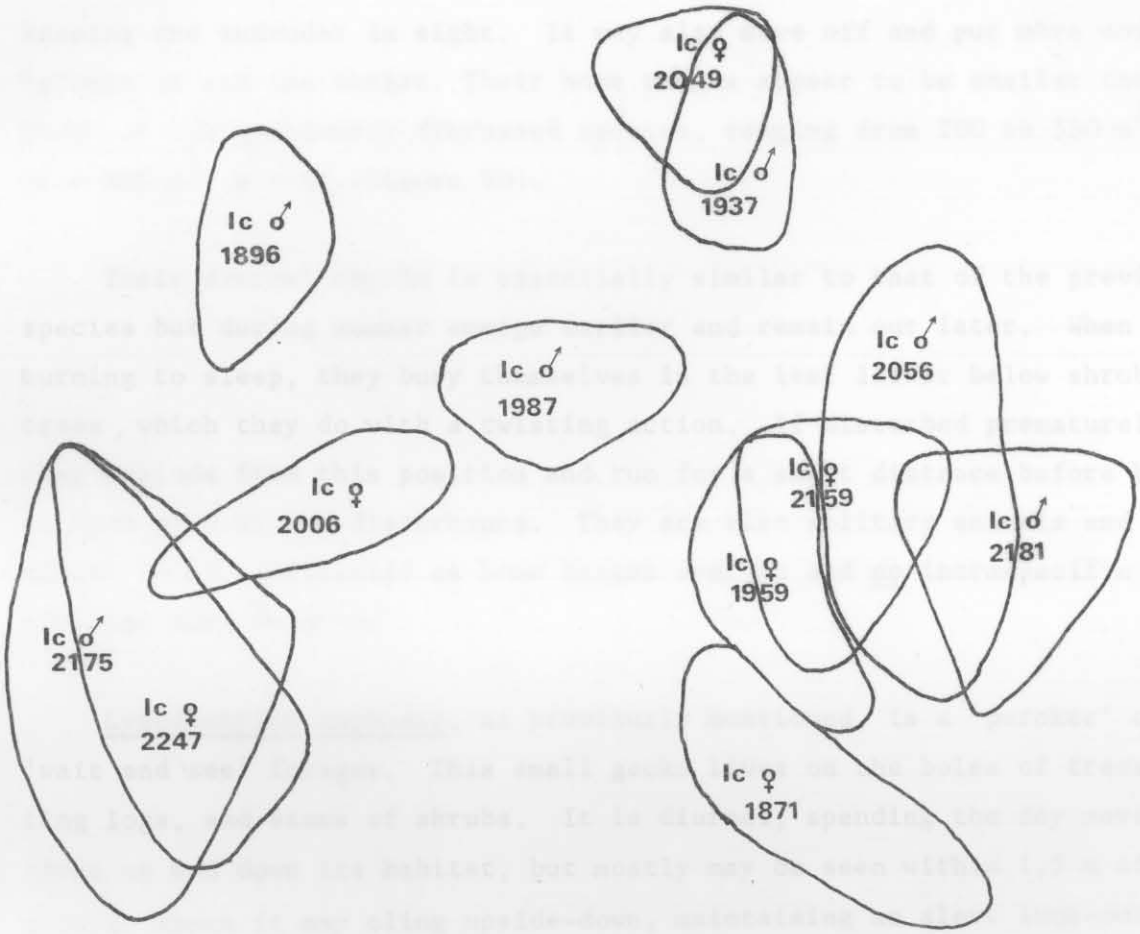
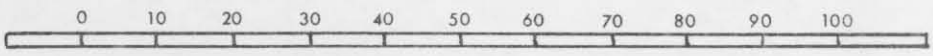


Figure 89. Home ranges of Ichnotropis capensis in the Burkea africana - Eragrostis pallens Study Area (A) 1976 (B) 1977.

B





Scale in metres

During the heat of the day, i.e. 12h00 -14h00, these lizards stayed in the shade of shrubs and if disturbed ran swiftly off but returned to shade as soon as possible. They begin foraging during summer at 07h00 and apart from the noon period, are active until 17h00. During the winter, the few individuals which are active, emerge later and are already dormant by 16h00. The lizards live down burrows and partially bury themselves in the loose soil under logs where they lie semi-curled up and become almost totally torpid.

In contrast to the foraging strategy of the previous lizard, Mabuya varia (variable skink) is intermediate between the 'active' forager and the 'passive forager, such as the Cape dwarf gecko. It therefore hunts as well as 'hawks'. Its movements are usually in the form of a short, fast dash across open ground, taking cover under grass clumps, logs, shrubs and rocks, which it then uses as vantage points from which to survey the surrounding area. The boles of trees are frequently used for this purpose to a height of one metre, but more often lower down. If threatened, it does not hesitate to climb up into the branches of the tree, while on rocky outcrops it always manoeuvres around to the rock face away from the threat. From this situation they may look at the intruder and provided this does not come closer, will become inquisitive and lie on the rock, but always keeping the intruder in sight. It may also move off and put more cover between it and the threat. Their home ranges appear to be smaller than those of the previously discussed species, ranging from 200 to 550 m^2 ($\bar{x}$ = 389 m^2 n = 5), (Figure 90).

Their diurnal rhythm is essentially similar to that of the previous species but during summer emerge earlier and remain out later. When returning to sleep, they bury themselves in the leaf litter below shrubs and trees, which they do with a twisting action. If disturbed prematurely, they explode from this position and run for a short distance before halting to look back at the disturbance. They are also solitary animals and do not appear to be territorial as home ranges overlap and no intraspecific aggression has been observed.

Lygodactylus capensis, as previously mentioned, is a 'percher' or 'wait and see' forager. This small gecko lives on the boles of trees, rotting logs, and stems of shrubs. It is diurnal, spending the day moving about up and down its habitat, but mostly may be seen within 1,5 m of the ground, where it may cling upside-down, maintaining an alert look-out for

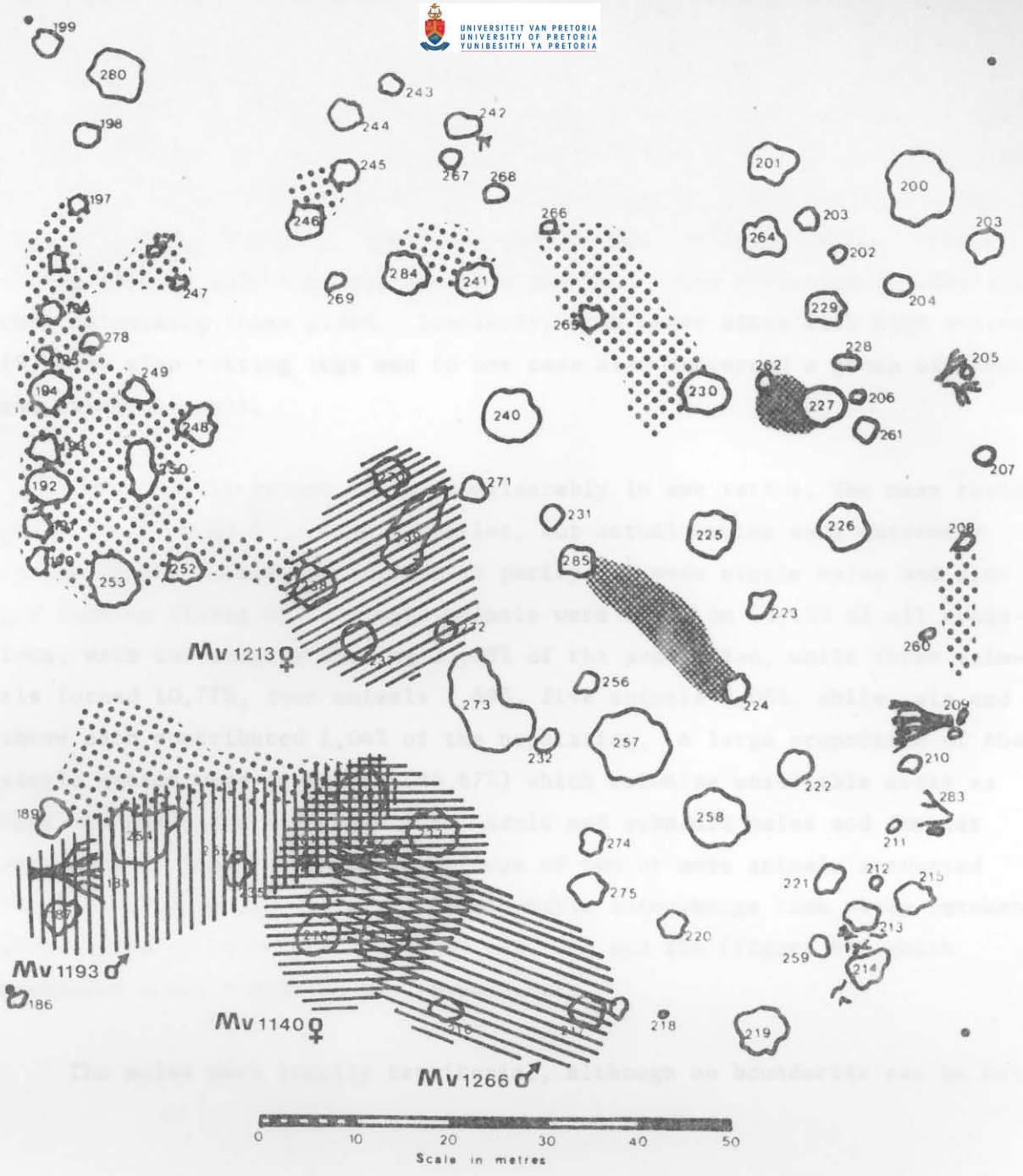


Figure 90. Home ranges of Mabuya varia within the Lygodactylus capensis Intensive Study Area.

passing prey. Once movement is sighted, it may dash down and snap up its prey as much as 60 cm from its retreat.

They appear to prefer trees such as Burkea africana, because these are normally partially rotten and woodboring beetles have excavated numerous tunnels while there is usually much loose bark under which the lizards can hide. It has already been mentioned that in an area of one hectare, these geckos occupy 69% of all the trees, but 100% of all the available habitat. Adults keep to the best sites while the juveniles frequently are found in shrubs where they sleep at the base in the leaf litter addressed to the stem. The adults live in the holes and crevices of the bole. As such, the Cape dwarf gecko lives in small family groups with a mean of 2,49 (n = 172) individuals per site. However, when assessing the numbers of individuals captured at each number over a six-month period, then a different picture is apparent. Single animals occur with the greatest frequency followed by pairs, threes and fours respectively. The largest number of individuals captured at any one site was 13, which was a rotting Lannea discolor log which had been chopped down while surveying lines during 1974 or approximately one year earlier. This indicates to what extent colonising takes place. Similarly, both other sites with high values (9) were also rotting logs and in one case also concerned a group of trees and shrubs as well.

These family groups varied considerably in sex ratios. The mean ratio was 1,00 ♂ : 0,63 ♀ : 0,32 juveniles, but actual ratios were extremely varied from 5,0 males per female to parity and even single males and single females (Table 48). Single animals were found on 46,15% of all occasions, with two animals forming 23,08% of the population, while three animals formed 10,77%, four animals 7,69%, five animals 3,08%, while six and above each contributed 1,04% of the population. A large proportion of the single geckos were juveniles (26,67%) which colonize unsuitable areas as they are small and inconspicuous. Adult and subadult males and females were equally single. Therefore groups of two or more animals accounted for 53,85% of the population. Considerable interchange took place between sites close to each other, such as nos. 213 and 214 (Figure 91) which harboured 8 and 9 individuals respectively.

The males were locally territorial, although no boundaries can be de-

Table 48. Adult and juvenile complement of Lygodactylus capensis inhabiting different sites in the Intensive Study Area : June - December 1975.

Number of sites	Number of adult males	Number of adult females	Number of Juveniles
1	7	2	0
1	3	1	0
1	5	1	2
1	4	1	0
3	1	1	0
3	0	2	0
1	4	3	0
6	2	0	0
11	1	0	0
1	6	6	1
1	4	1	1
2	2	1	0
11	0	1	0
1	2	2	0
1	2	0	1
1	3	2	0
2	1	1	1
1	3	5	2
1	1	1	2
1	0	0	2
1	1	0	2
8	0	0	1
1	1	2	1
1	1	0	1
1	3	0	0
1	2	1	1
1	0	1	1
66	84	53	27

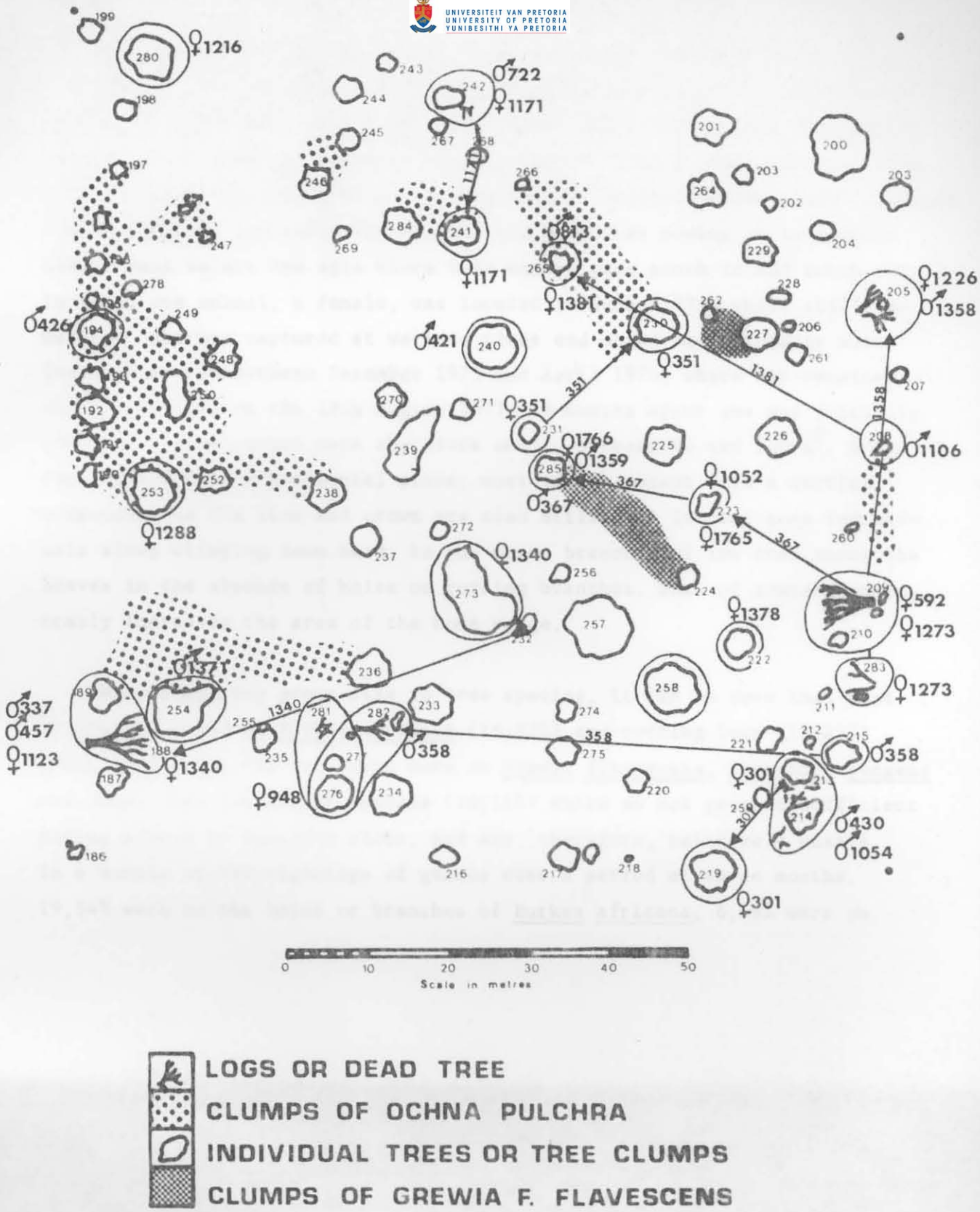


Figure 91. Home ranges and movement of marked Lygodactylus capensis in the Intensive Study Area.

fined as the only interactions seen were in close proximity of a basking or foraging adult. He would threaten all who came close by raising his body, blowing out his gular region and lashing his tail. If this display did not succeed, then he would advance on the intruder and if the latter did not flee, then a lateral threat posture was assumed followed by an attack. The animals grasped any portion of the body, frequently the tail or leg and attempt to overthrow the opponent. Once one individual had surrendered it would flee only to be pursued extensively by the victorious male. There is what amounts to be a hierarchical system operating, with the dominant males and females having the most favoured basking and foraging sites, while the remainder are scattered elsewhere.

While most individuals stayed at one site, occasionally moving to another close by site from 10 to 20 m away, on some occasions individuals moved distances of 50 m or more. The reason for such moves is not readily apparent. In some instances, a juvenile grows up in a small shrub or tree which is then unsuitable for the adult and it therefore moves until it finds a site. Here it may abide for several months before moving on to another site. Many select one site where they may be seen month in and month out. In fact, one animal, a female, was located in June (1975) while still immature. She was captured at various times and moved to a probably more favourable site between December 1975 and April 1976, where she remained until last seen on the 19th August 1977, 26 months after she was initially captured. Home ranges were therefore small, between 40 and 100 m^2. However, apart from a horizontal plane, most of the geckos have a vertical component, as the stem and crown are also utilized. In fact some individuals sleep clinging down head, to the upper branches of the tree among the leaves in the absence of holes or rotting branches. This of course considerably increases the area of the home range.

When comparing group size to tree species, it can be seen that most groups are found on Burkea africana (16,92%) and rotting logs (13,85%) while single lizards are found more on Grewia flavescens, Strychnos pungens and other less favourable species (26,15%) which do not present sufficient hiding places or roosting sites, and are, therefore, relatively unsafe. In a sample of 329 sightings of geckos over a period of three months, 19,54% were on the boles or branches of Burkea africana, 6,69% were on

Terminalia sericea, 4,56% on Strychnos pungens, 2,13% on Ochna pulchra with various other species occurring in the one hectare study plot in lesser amounts. However, the overwhelming majority choose to spend the day on rotting logs mostly lying on the ground but also dead trees upright. Sixty-two percent of the geckos were found in these situations. However, many of these were small logs lying at the foot of trees or bush clumps, but at the same time those found on living trees and shrubs were often on dead branches or other dead wood. It is significant that they actually choose the rotting logs as these provide better shelter, not camouflage as the boles of Burkea, Terminalia and others, match the colour of the geckos, which in any event are also capable of colour change by lightening or darkening the skin to suit the background. There is probably an additional advantage in that there are numerous insects and other arthropods found around rotting logs, therefore supplying food as well, such as beetles, ants and spiders, which feature prominantly in their diet (Figure 32).

It was seen on examination of stomach samples that feeding activity took place mainly during the afternoon (Figure 34). This observation is supported by the general activity pattern of the geckos which indicates a period of greater activity during the late afternoon (Figure 92) based on the numbers of geckos per minute during the gecko-sampling periods.

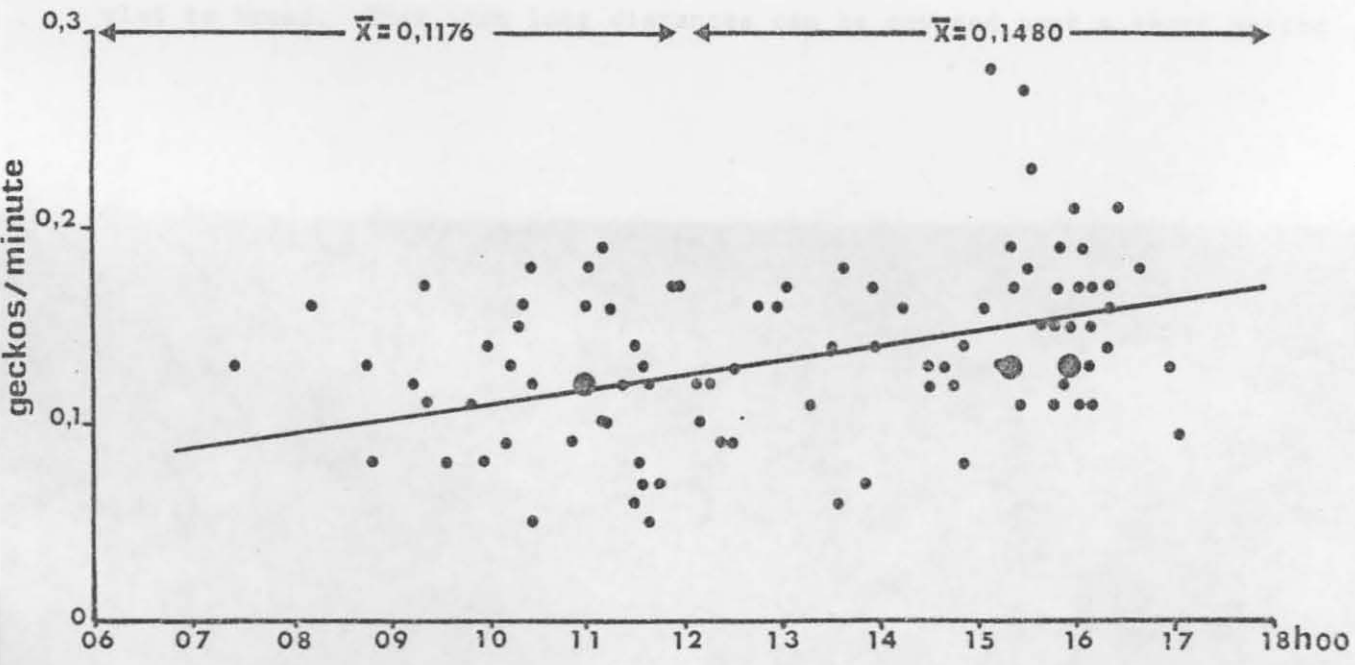


Figure 92. Correlation of activity of Lygodactylus capensis with time of day in the Study Area.

Although Panaspis wahlbergi were relatively common in the Study Area, no details of movements could be determined because of the infrequency of capture. They do, however, appear to be local and probably do not have large home ranges.

Similar comments are pertinent for the remainder of the lizard species of which some, such as Pachydactylus bibronii left their rocky retreat for up to four metres, being captured in traps that distance away. This means that foraging takes place some distance from the rocky outcrops. During the day they are restricted to crevices between rocks which they live in, in pairs or small groups.

Lygosoma sundevallii was also not captured with any frequency but was determined to be nocturnal as they were only captured in the traps during the night while tracks also indicated nocturnal movement. These lizards are sand dwellers, living under rotting logs and stones during the day but emerging by night to change location and forage.

Amphibians

Although movement by amphibians and in particular Bufo garmani and Kassina senegalensis took place, recaptures were few and only supported the allegation that they move between the turf vlei and the Study Area. No trapping was carried out between the Study Area and the vlei. This can be seen in Table 49 from which it is apparent that despite the paucity of recaptures, a trend is visible. Activity during the months, August, September, and to a lesser degree, October and November, appears to be downslope, that is towards the turf vlei, while during middle and late summer, the reverse situation is noted. This pertains only Bufo garmani, as movement by Kassina senegalensis appears to be random.

It is also apparent that some of the movements took place over considerable lengths of time. This further confuses the issue, as obviously no movement took place during the four dry and cold months of the year, so that the distances covered could have been prior to hibernation or they could have been thereafter. The time of activity was always used as the time of recapture and, therefore, no finite conclusions can be made, but merely serves to indicate support for the theory that they go to the turf vlei to breed. That such long distances can be covered over a short period

of time is evidenced in Table 49 and distances of over 100 m per day are by no means unusual.

It is also apparent that in several instances recaptures were effected in the same place despite long time intervals, which indicates some homing ability. This is supported by Taylor (loc.cit.) who tested toads' homing capabilities. He obtained 57 recoveries involving 36 Bufo garmani after release at the site of capture. He went on to release these toads at varying distances from their original capture site and returns involved distances of 500 to 1 000 m in various directions. In some instances, the toads covered the 500 m in from two to four days, and one released 1 000 m away was back home in five days. Another took 209 days before it eventually arrived back. There is, therefore, no doubt that a homing instinct exists, although the recovery rate was considerably less with 12 recoveries involving nine individuals. What is unusual is that all such recoveries were males and that they had to circumvent several obstacles including ponds where other individuals were calling.

The kassinas were also capable of long distance movement over short periods of time (Table 50). Movement appears to be somewhat random and in fact rarely westwards towards the turf vlei, which is an interesting phenomenon, but for which there is no explanation except that other breeding sites must also be available. None are found in the Ecosystem Study Area as a whole. Movements may, therefore, be more extensive than originally thought. It is possible that a large scale flux of these frogs takes place and this involves large scale replacement of individuals annually.

Table 49. Movement of Bufo garmani in the Burkea africana - Eragrostis pallens Study Area from recapture results : May 1975 - May 1977.

Date	Distance (m)	Direction	Time (days)
November	325	SW	35
	100	W	35
December	100	E	39
	500	E	22
	100	E	18
January	0	same place	31
	100	E	3
	0	same place	54
February	62	SW	28
	40	NE	2
	100	E	2
	420	E	24
	430	E	3
	600	S	23
	0	same place	25
	0	same place	31
	230	E	3
	0	same place	28
	26	NE	6
	0	same place	1
	80	E	3
	21	SE	2
March	0	same place	2
	75	W	23
	375	E	24
	15	E	2
	100	ESE	24
	535	NNE	27
	325	E	27
	60	S	27
April	65	SW	4
	130	S	39

Date	Distance (m)	Direction	Time (days)
May	20	E	41
August	10	SW	2
September	540	W	317
	290	E	213
	0	same place	2
	45	SW	29
	15	W	2
	60	NW	1
	10	SW	154
	5	SW	220
	121	SW	5
	10	W	213
October	90	W	195
	500	NNW	218
	230	E	219
	100	E	6
	55	SW	196
	280	SW	6
	20	E	215
	25	W	2
	100	W	2
	130	E	2
	40	S	26
	100	S	4
	20	SE	5
	35	NE	5
	40	E	29
	46	E	30

Table 50. Movement of Kassina senegalensis in the Burkea africana - Eragrostis pallens Study Area from recapture results.

Date	Distance (m)	Direction	Time (days)
November	55	NE	2
"	12	NE	2
"	0	same place	2
"	35	SE	28
December	425	SE	23
"	200	SE	7
January	370	E	49
"	0	same place	2
"	22	SE	2
"	100	S	2
February	200	S	5
	140	SE	391
September	450	N	241
October	150	ESE	244
	200	NNE	5
	10	N	2
	20	SW	22
	60	N	21
	0	same place	2
	230	W	2
	200	N	2
	135	NE	3
	200	E	2
	100	E	2
	375	SE	5
	80	Se	5
	70	SW	5
	34	SE	5
	50	N	7