POPULATION DENSITY AND SOCIAL ORGANISATION OF THE CAPE CLAWLESS OTTER, AONYX CAPENSIS SCHINZ, IN THE TSITSIKAMA COASTAL NATIONAL PARK

by

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Submitted in partial fulfilment of the
requirements for the degree of

M.Sc.

in the Faculty of Science
UNIVERSITY OF PRETORIA
PRETORIA

JULY 1983

To Paul, Ann and Caroline

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ABSTRACT

A survey of the 58,5 km of coast within the Park revealed a total of 120 holts with a tendency towards even spacing and a mean nearest neighbour distance of 350 m. 56% of spraint sites were within 50 m of holt.

Faecal analysis revealed significant spatial variation in dietary composition within the Park. In terms of calorific value fish are at least as important as crabs in the diet.

Collection of radio-actively labelled faeces (spraints) from three otters released on two separate sections of coast provided an estimate of population density - 0,52 otters km^{-1} of coast. Population size for the whole Park was estimated at 30-31 otters. The minimum extent of one labelled female's range was 14,3 km.

Most radio-tracking data were obtained from three adult males. These animals, tracked in winter, spring and summer, were predominantly nocturnal. Dougal, tracked for two and a half months, had a range of 19,5 km of coast, a home range of 15,0 km and a core area of 8,5 km. Three other adult males had minimum ranges of 8,5-13,3 km.

Four adult males shared a common range and the holts within it. They were seen to forage together. This group of four was designated a clan. A central section of the clan range, coinciding with Dougal's core area, appears to be a clan territory.

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ACKNOWLEDGEMENTS

The following organisations and people lent assistance during the project for which I am very grateful.

Professor J.D. Skinner who gave support and advice throughout the project in his capacity as my supervisor. I am also grateful for the great hospitality that he and his family, particularly Patsy, extended to me throughout my stay in South Africa.

The National Parks Board for their permission to work in the Tsitsikama Coastal National Park. Dr G.A. Robinson whose enthusiasm, advice and cooperation, including the loan of his home at Nature's Valley, were invaluable.

At Tsitsikama the warden, Dennis Bower and the staff were invariably friendly and provided much cheerful cooperation during the project. I'd particularly like to thank John Allen, the Nature Conservation Officer, and Peet Joubert, the Information Officer for their help and their respective families for unfailing hospitality. Dr Nic Hanekom supplied me with climatological data for the Park. The Game Rangers, in particular Georgie Mordeka, Gilbert Xashimba and Alfred Champion, who helped in the transport of caracal traps and reported otter sightings.

From the Mammal Research Institute Dr Neil Fairall provided valuable assistance in the field, in obtaining permits to use $^{65}ZnCl$ and during the write-up of the thesis. Rudi van Aarde placed orders and corresponded with the suppliers of my radio-tracking equipment. Peter Apps checked my first draft and made invaluable suggestions for improvements in the text. Dr R.H.N. Smithers provided me with copies of the text and figures relating to Aonyx from his forthcoming book "The Mammals of the Southern African Subregion".

The Cape Provincial Administration, Department of Nature and Environmental Conservation loaned two caracal traps.

Adam and Dorothy Mecinski at Cape Point Nature Reserve gave me the opportunity to examine their tame otter.

Dr André Reitz at Knysna who performed the intraperitoneal implant of the radio-transmitters efficiently for a minimal fee.

Douwe van der Zee with whom I was able to discuss many of the aspects of working on Aonyx.

Dr Graham Ross of Port Elizabeth Museum provided the identification cards of fish bones, enabling me to include a section on feeding ecology. Messrs C. Buxton and M. Smale, of the same institution, provided references and advice during the write up of my thesis.

Professor T. Erasmus of the University of Port Elizabeth and Dr H.C. Potgieter of the University of Pretoria gave me access to gamma counters and instruction in their use.

Miss J.B. Walker kindly identified ectoparasites collected from otters.

Mr N.G.N. Swart of the Statistics Department of Pretoria University helped me with my statistical problems.

Amanda Nel prepared many of the figures which appear in the text.

Mr J.J. Booysens of the Geography Department, University of Pretoria provided valuable assistance with the preparation of maps.

And finally Ingrid Vis who waded through mounds of barely legible script to complete a neatly typed thesis.

INTRODUCTION

The sub-family Lutrinae is comprised of twelve species grouped into five genera. Otters have a worldwide distribution, being absent only from the polar regions, Australia, Madagascar and arid regions (e.g. the Sahara and Gobi deserts). Little is known of these members of the mustelid family, largely due to the shy and elusive habits of these animals. This necessitates the use of recently developed techniques such as radio-tracking for in depth study of their behaviour and ecology. Even today the majority of the existing data on otters pertain to feeding ecology and have been collected by faecal analysis.

Perhaps in part due to the paucity of available information, otters are regarded as among the most susceptible mammals to changes in their environment. Of the twelve species six are covered by the U.S. endangered species act, 1973 (three of these are listed as vulnerable or endangered in the IUCN Red Data Book, 1981) and a seventh is not covered by the US endangered species act but is listed as endangered in the IUCN (International Union for the Conservation of Nature and Natural Resources) Red Data Book.

The major threat to otters appears to be water pollution, which has been cited as the major cause of the decline of the European otter, Lutra lutra in Britain (Chanin & Jeffries, 1978), Sweden (Erlinge, 1971) and France (Green & Green, 1981). Loss of terrestrial habitat by destruction or modification (MacDonald, Mason & Coghill, 1978) and direct persecution for pelts or as pest species constitute additional pressures. In the case of the sea otter Enhydra lutris, persecution for the pelt alone reduced the animal to the verge of extinction (Kenyon, 1971).

In South Africa, rapid industrial and agricultural growth dictates that all three pressures are increasing on the Cape clawless otter, Aonyx capensis, Schinz 1821. Reliable data are too scarce to determine the status of Aonyx. Though it is still common in some parts of the country, the status of Aonyx may deteriorate rapidly in the face of this combination of pressures. This was certainly the case with the European otter, Lutra lutra, in Great Britain (Chanin & Jeffries, 1978).

Little is known of the behaviour and ecology of Aonyx capensis and the majority of work so far has been performed in South Africa. Until the seventies only popular accounts (Carter 1956, Eyre 1963) and general notes (Fitzsimons 1919, Shortridge 1934, Dorst & Dandelot 1970) on Aonyx had been published. Tayler 1970 was the first to record Aonyx in a marine habitat but their occurrence on the Tsitsikama coast was common knowledge in the area prior to this publication.

Rowe-Rowe (1977a, b & c) published work on the feeding ecology and predatory behaviour of Aonyx in Natal. To date the major work on Aonyx has been published by van der Zee (1979, 1981 a & b) from the Tsitsikama coast. Most of his data related to feeding ecology though he did make an estimate of population density (33 otters on 59 km of coast) which agrees very closely with estimates arrived at in the present study using a more sophisticated technique. Van der Zee's main conclusions were that Aonyx is an opportunistic feeder in the Tsitsikama region, consuming more than 34 species of prey animal. Four species, the red rock crab (Plagusia chabrus), the brown rock crab (Cyclograpsus punctatus), the octopus (Octopus granulatus) and the suckerfish (Chorisochismus dentex) constituted 81% of all prey taken (86% biomass). The remaining 19% of prey taken (14% biomass) consisted of over 30 species, at least 20 of them fish (van der Zee, 1981). There appeared to be no pattern in the monthly variation of the importance of different prey items.

From records of tracks and sightings, van der Zee was able to give minimum home range estimates, for two females with cubs, of 5 and 6,5 km respectively. Inability to mark animals for field recognition and their general elusiveness precluded further data on social organisation from being gathered.

Given the paucity of data available on Aonyx and the mounting pressures on this species it is becoming vital to assess the potential of reserves, such as the Tsitsikama Coastal National Park, to maintain a viable population of Aonyx capensis. Such reserves may eventually be the only conservation measure capable of preventing the extinction of Aonyx in South Africa.

The viability of a local population in its natural, essentially undisturbed habitat is dependent to a large extent on the size of that population (Shaffer, 1981). Thus in assessing the potential of reserves it is vital to obtain an estimate of population size. The latter estimate will be an important factor in the planning of future reserves for the species.

In more specific terms it is necessary to define the food requirements of the species as far as possible and then to estimate food availability in the reserve. The ability to link food availability with population density of Aonyx would be invaluable in the assessment of potential reserves.

Social organization is linked to ecological factors and studies of the former will often lead to a better understanding of the latter. In particular it has been shown for a number of birds (Orians 1961, Krebs 1971), mammals (Healey 1967, Carl 1971) and other animals that territorial behaviour can limit population density on a local scale. The implications of this for reserves of limited size could be serious.

In the long term if the social organization of a species can be related to the ecology of the animal in that area it may then be possible to make predictions on social organization and thus, for example, population density in ecologically dissimilar areas. This would be of considerable value in evaluating the potential of an area as a reserve for the species if the animal is absent or is known to be temporarily depleted in that area.

The behavioural and ecological data collected in the course of the study are integrated to investigate the behavioural adaptations of *Aonyx* to a marine habitat. The findings of authors working on other otter species (e.g. Erlinge 1967b and 1968b, Watson 1978, Kruuk & Hewson 1978 and Loughlin 1980) in different habitats provide insights into the selective pressures that shape the behaviour and social organization of *Aonyx*.

It has been suggested by Watson (1978) that in Britain the coast is the optimum habitat of *Lutra lutra*. The reason for this suggestion is the higher density of otters in British coastal habitats (Watson 1978, Kruuk & Hewson 1978) compared to freshwater habitats in Sweden (Erlinge 1968). The present study provided a population density estimate for *Aonyx* in a marine habitat which could be compared with that of other otter species in freshwater and marine habitats. A similar estimate for *Aonyx* in a freshwater habitat could give an indication of the optimum habitat of this species and possibly its evolutionary origins too.

To summarise, the main objectives of the study were:

(i) to examine habitat utilisation, foraging behaviour and social organization of *Aonyx capensis* in a marine habitat, with particular reference to the degree of territoriality displayed;

(ii) to make an estimate of otter population density within the Tsitsikama Coastal National Park;

(iii) to make an incidental study of the spatial variation in the composition of prey species within the Tsitsikama Coastal National Park.

TAXONOMY

Order	Carnivora
Suborder	Fissipedia
Family	Mustelidae
Subfamily	Lutrinae
Genus	*Aonyx* (Lesson 1827)
	Aonyx capensis (Schinz, 1821)

Smithers (in press) provides the most up to date taxonomy for this species. There are two species in the genus, both restricted to the African continent. *Aonyx capensis*, the Cape clawless otter is slightly smaller than *Aonyx congica*, the Zaire clawless otter. The most important difference between the two species are the much smaller cheekteeth of *A. congica* compared to *A. capensis*. There is also more white in the pelage of *A. congica*. This species is apparently restricted to the Congo basin (Coetzee, 1977a).

Three subspecies of *A. capensis* were recognised by Coetzee (1977a): *A. c. capensis* from the Southern African Subregion, *A. c. meneleki* (Thomas, 1903) from Ethiopia, and *A. c. hindei* (Thomas, 1905) from East Africa, eastern Zaire and possibly Zambia.

DISTRIBUTION

Aonyx capensis is found throughout sub-Saharan Africa with the exception of arid regions and the Congo basin where it is replaced by *Aonyx congica* (Fig. 1). The absence of the species from the Zambezi valley east of the Victoria Falls which may be due to a high population density of crocodiles (Ansell, 1978) but the gap in the distribution in northern Mozambique is probably due to lack of collecting (Smithers, pers. comm.).

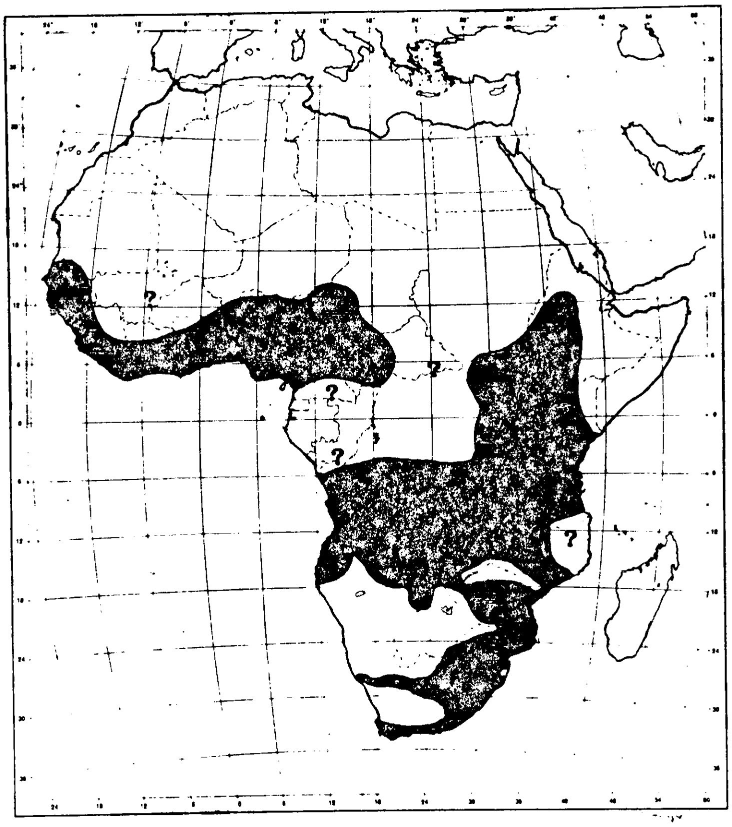


Fig. 1 The distribution of Aonyx capensis (Schinz, 1821) in Africa, Smithers (in press)

A. capensis is invariably associated with the presence of a permanent supply of freshwater (rivers, lakes, streams, swamps etc). This species has often been observed on the sea coast in West Africa (Rosevear, 1974) and in South Africa has been observed on the coast from the south-western Cape to northern Natal (van der Zee, 1979). Freshwater populations occur throughout most of the Transvaal, Orange Free State and Natal but only along the Orange River and the southern and eastern regions of the Cape Province. A. capensis is absent from the north-western Transvaal, north-eastern Natal and a large part of the Karoo.

STUDY AREA

The Tsitsikama Coastal National Park lies on the southern coast of the Cape Province between 23°30'E and 24°15'E. The Park comprises 58,5 km of coast, the boundaries lying at the two Groot Rivers at Nature's Valley and Oubosstrand (Fig. 6).

Topographically, the Park consists of the scarp slope of a wave cut platform which rises steeply from the sea. The escarpment is about 180 m high at the coast and extends a further 5-8 km inland to the foot of the Tsitsikama Mountains. Within the Park five large rivers have cut deeply into the escarpment and many small rivers and streams flow over the edge. The bedrock of the escarpment consists largely of sandstones and shales of the Gamtoos, Table Mountain and Bokkeveld series (Toerien, 1976).

The climate is mild in comparison with that of much of the remainder of the Southern African sub-region. Rainfall is evenly distributed throughout the year with only small peaks in spring and autumn (fig. 2). Mean annual rainfall is higher inland, Storms River Forestry Station on the plateau receiving a mean annual rainfall of 1 119 mm (1883-1975), whereas Storms River Mouth had a mean annual rainfall of 1 001 mm between April 1974 and March 1982.

The mean daily minimum temperature ranges from 7°C in August to 18°C in January, and mean daily maximum ranges from 12°C in June to 24°C in January. Temperatures never fall below freezing point in the Park (fig. 3). Mean monthly sea temperature varied from 15°C to 22°C during the study. Sea temperature dropped as low as 11°C in some months (Fig. 4).

Acocks (1975) classifies the veld type of the Park as Coastal Tropical Forest, specifically Knysna forest. Within the Park the dry forest, which includes over 100 species of trees, is interspersed by patches of

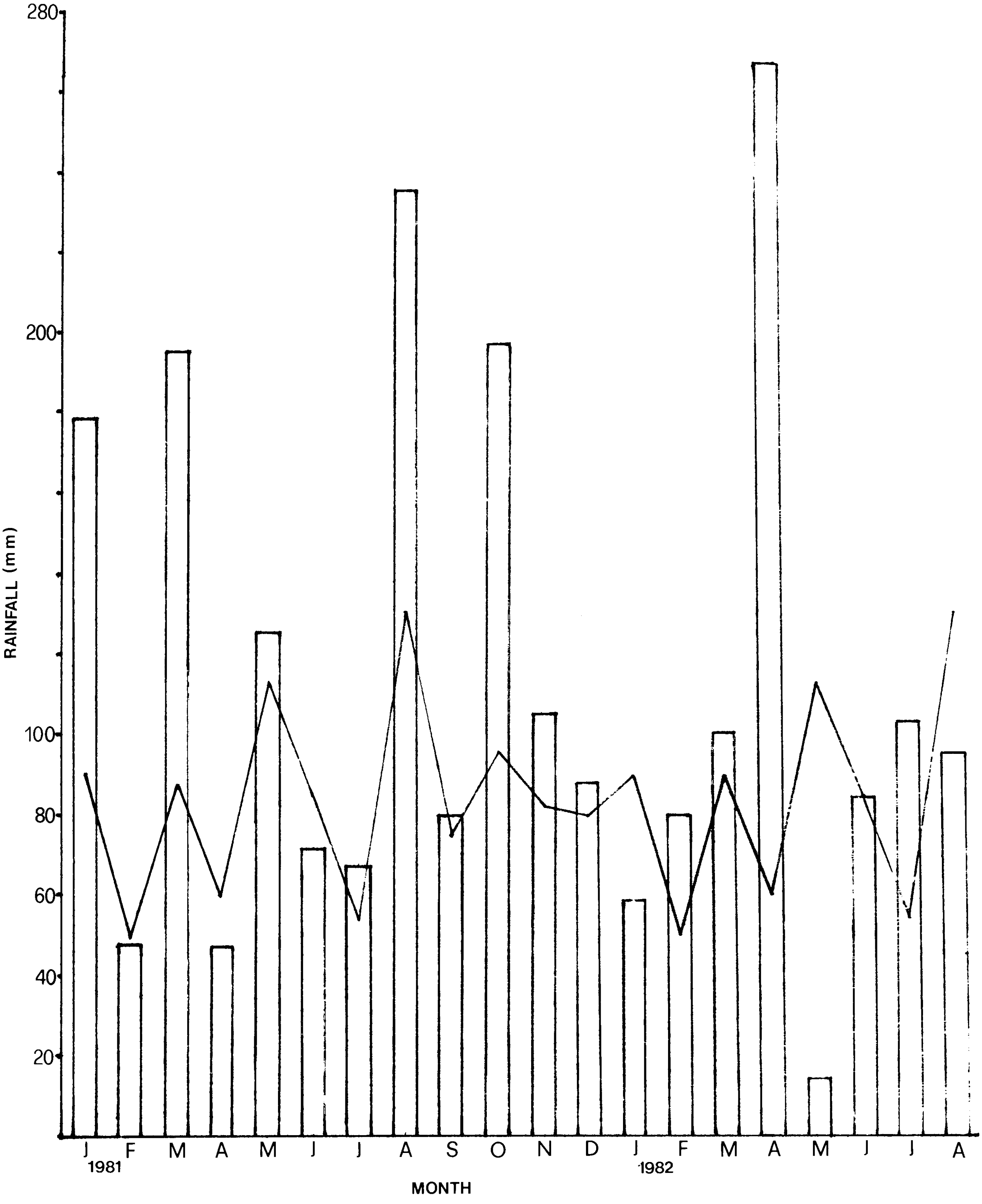
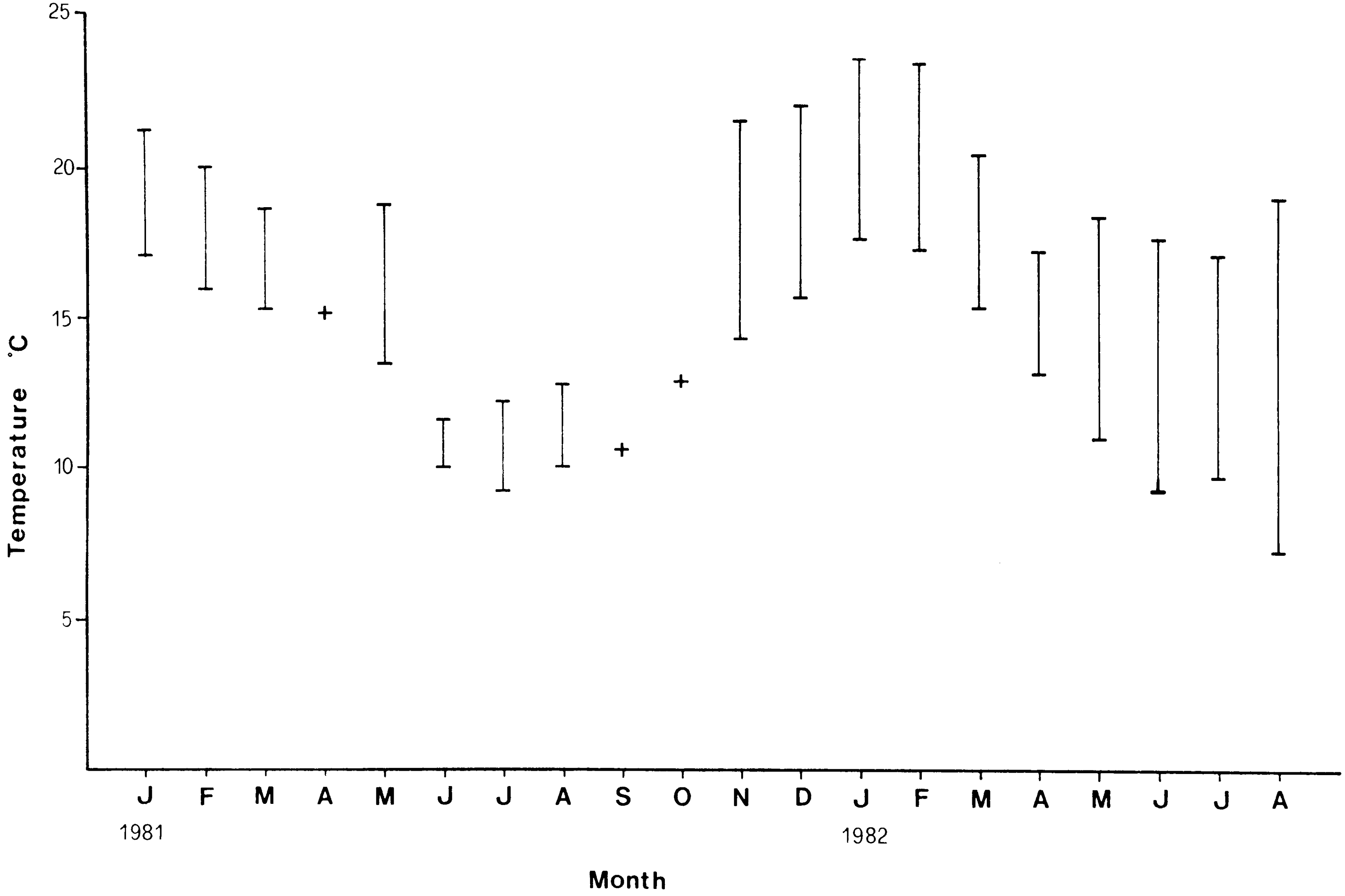


Fig. 2 Monthly distribution of rainfall at Storms River Mouth.

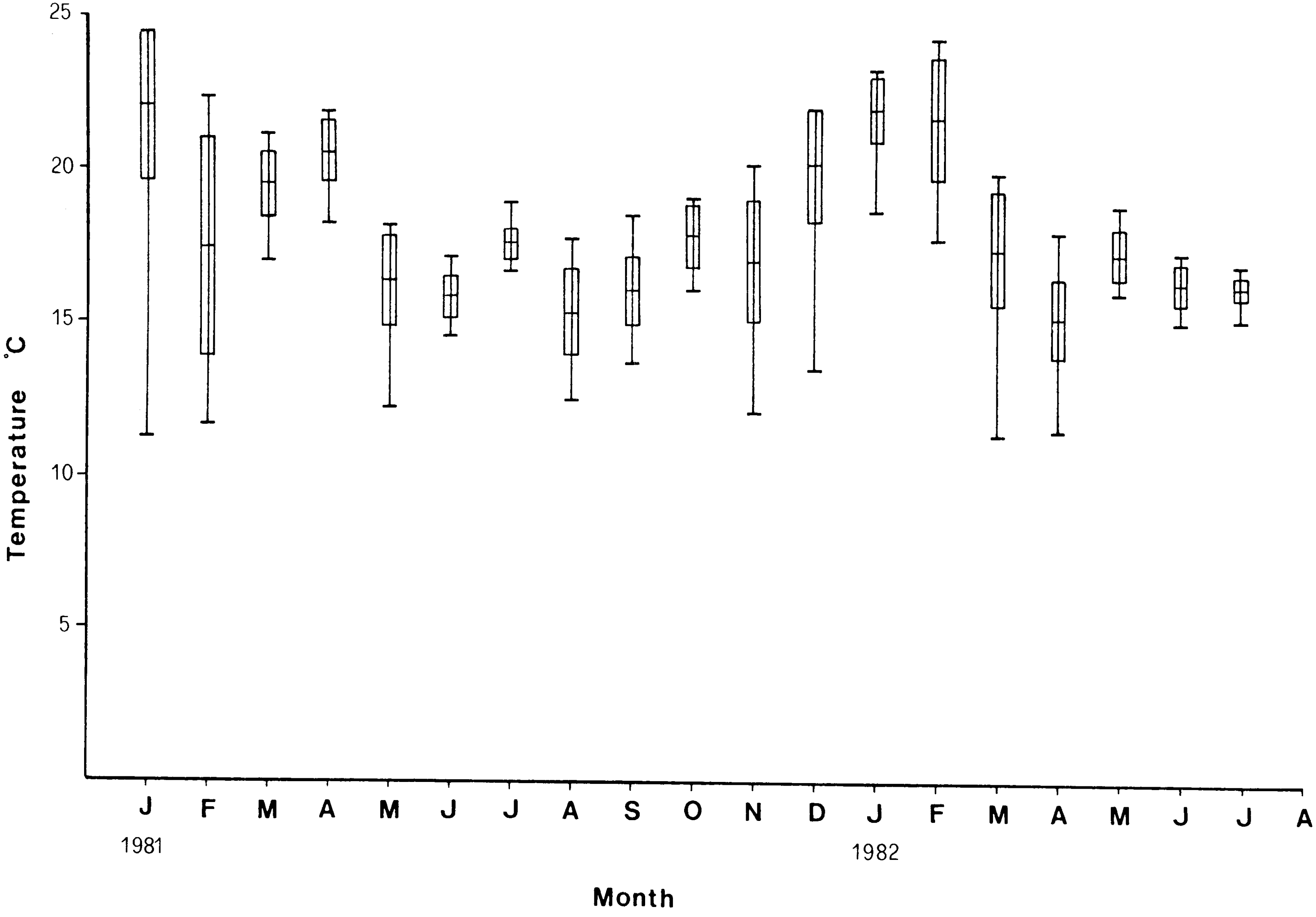
Histogram: monthly rainfall at Storms River Mouth during the study period

————: mean monthly rainfall at Storms River Mouth from April 1977 to March 1982 at Storms River Mouth during the study period



with their standard deviations recorded at Storms

River Mouth during the study period



low scrub-bush and macchia scrub (Fynbos) with or without proteas (Skead & Liversidge, 1967). The top of the escarpment is covered by macchia, moist forest and pine plantations. A detailed description of bush and forest in the area may be found in von Breitenbach (1974).

Larger mammals seen in the Park in the course of the study were bushbuck, *Tragelaphus scriptus*, blue duiker, *Cephalophus monticola*, baboon, *Papio ursinus*, vervet monkey, *Cercopithecus pygerythrus*, bush pig, *Potamochoerus porcus*, porcupine, *Hystrix africaeaustralis*, the large-spotted genet, *Genetta tigrina*, the Cape grey mongoose, *Herpestes pulverulentus*, and the ratel, *Mellivora capensis*. Tracks identified during the study indicated that the water mongoose, *Atilax paludinosus*, was very common in the Park and caracals, *Felis caracal*, and leopards, *Panthera pardus*, were also present.

METHODS

The data collected in the course of this study can, on the basis of origin, be split into two broad categories. The first category is indirect evidence collected by examination of otter sign (spraints, tracks, rolling places and the lie-ups known as holts) and detailed analysis of the spraints to yield information on feeding ecology.

The second category is direct evidence collected by trapping and marking the animals using a variety of techniques, namely metal ear tags, plastic ear tags, red dye, implanted radio-transmitters and intramuscular injections of radio-isotopes. The data are accumulated by subsequent trapping and observation of the marked animals and recovery of radioactively labelled spraints. A further contribution came from sightings of unmarked and therefore unidentified otters. Independent observer sightings were accepted if they could be confirmed.

To obtain as full a picture as possible of the behaviour and ecology of *Aonyx capensis* on the Tsitsikama coast, results obtained from the various techniques are pooled and analysed together. Studies such as Erlinge's (1967 and 1968) on the European otter, *Lutra lutra*, and Kruuk's (1978 a, b) on the European badger, *Meles meles*, have shown how different techniques serve to complement each other. A good example is the combination of radio-tracking data and food marking experiments seen in Kruuk's study.

COASTAL SURVEY

Tracks and sign have been used extensively in the study of otters largely because of the shy and elusive habits of these mustelids. For all otter species, with the exception of the sea otter, *Enhydra lutris*, observation in the wild is difficult and usually of short duration. Prolonged observation in the field has only been made possible by the recent development of radio-tracking.

In the course of the present study two complete surveys of the whole of the Tsitsikama coast were completed. The first survey was conducted between the end of January and mid-March 1981 and the second between the end of February and mid-March 1982. The first survey is of only limited value as the observer lacked experience in the detection of otter sign and holts. The second survey may be regarded as a reliable record of the occurrence and distribution of otter sign and holts on the 59 km stretch of coast in the Park.

The occurrence of fresh otter spraints and tracks was used to monitor the utilisation of holts along 6 km of coast between the beginning of February and mid-May 1981. The section of coast lies between George se baai, 4 km west of Stormsriver, and Steilkop 2 km east of Stormsriver (Fig. 5). As the first coastal survey and familiarisation with the study area were in progress at the same time, monitoring of the 6 km stretch of coast varied in intensity. However this section was searched at least once a week, usually twice a week and occasionally three times a week.

FEEDING ECOLOGY

The feeding ecology of Aonyx capensis on the Tsitsikama coast was studied extensively by van der Zee (1979). In the present study fewer spraints were analysed but collection sites were selected as a result of data arising from radio-tracking studies. At the time of collection, the two stretches of coast from which samples of spraints were taken, represented the known home ranges of two adult male otters. Unfortunately, the estimates of home range size were based on only two weeks of radio-tracking in each case.

One hundred spraints were collected from a 13 km section of coast between the Bloukrans and Geelhoutbos rivers (Fig. 5). A further 101 spraints were collected from a 10,5 km section between the Kleinbos River and Steilkop.

Another 20 spraints were collected from sites at least 400 m upstream of the mouths of the Bloukrans, Lottering and Elandsbos rivers. These spraints were not analysed as efficiently as the other 201 because they were the first to be processed. Apart from furnishing some data on the utilisation of rivers in the Tsitsikama, these spraints provided the initial experience in identification of prey remains. Thus any bias due to progressive improvement in the recognition of prey remains would be largely, if not entirely, confined to these twenty spraints. It was important to exclude such a bias from the spraints collected on the coast as in a sample of only 201 spraints changes in the accuracy of analysis could have had marked effects on the final result.

The main purpose of this analysis was to examine spatial variation in prey composition and not temporal variation, the latter having been thoroughly investigated by van der Zee. All the spraints were collected between 28th February 1982 and 8th March 1982.

Each spraint was collected in a small plastic bag numbered to identify the collection site and date. Once all the spraints had been collected each spraint was washed under a tap in a 600 µm sieve, to remove vegetable debris and other substrate particles, and then spread out to dry on newspaper.

Analysis of the spraints followed van der Zee (1979, 1981), with minor modifications:

(i) Hard parts of prey items were identified as far as possible.

(ii) The three main categories of prey remains namely *Plagusia chabrus* exoskeleton, *Cyclograpsus punctatus* exoskeleton and fish bones and scales, were weighed. The sum of these three categories gave the total weight of each spraint.

(iii) The chelae (pincers) of crabs, premaxillae of fishes and beaks of octopuses were measured, two dimensions being recorded for each item.

Identification of the fish bones was based on reference cards created by van der Zee. These consisted of the bones of identified prey species mounted on individual cards.

The analysis and presentation of the results were conducted along the lines set out by van der Zee (1979, 1981) to facilitate direct comparison.

The two principle methods of scat analysis were frequency analysis and bulk-weight analysis of identifiable hard parts in the spraints. Two types of frequency analysis were used:

(i) Percentage frequency - the number of scores of a prey species in a sample of spraints given as a percentage of the total number of spraints in that sample (van der Zee 1979, 1981).

(ii) Relative percentage frequency - the number of scores of a prey species in a sample of spraints given as a percentage of the total number of scores (van der Zee, 1979, 1981) of all categories in that sample.

Bulk weight analysis was achieved by direct weighing of each prey category. The categories were *Plagusia chabrus*, *Cyclograpsus punctatus* and all fish species. *Octopus granulatus* was excluded from the bulk-weight analysis as beaks are the only remains of this species found in the spraints. The fish remains were not weighed separately as species as the majority of fish bones were unidentifiable to species level. In the final analysis estimates of live weights of fish species taken were made using estimated numbers rather than dry weight of hard parts in the spraints (see below).

In the analysis of the results I employed a number of regressions and ratios calculated by van der Zee (1979, 1981). The regressions computed were between the sizes of the main prey organisms and the sizes of certain of their identifiable remains found in spraints. The ratios used were of live weight to weight of hard parts, calculated for a number of prey species. Details of the calculation are given in van der Zee (1979 and 1981).

Conversion factors used for calculating live weight from weight of prey remains in spraints are listed below, after van der Zee (1979, 1980).

TABLE 1
Conversion factors for weight of prey remains in spraints : live weight of prey consumed (van der Zee 1979, 1981)

PREY SPECIES	RATIO WT. IN SPRAINT : LIVE WEIGHT
Plagusia chabrus	1 : 5
Cyclograpsus punctatus	1 : 5
All fish	1 : 18.7

The live weight of individual fish species taken by otters was calculated using conversion factors based on mean live weight for each species. This was extracted from table 15 in van der Zee (1979) where an estimated live weight is calculated for a given number of individuals, estimated from the recognizable remains in spraints. Thus for Diplodon sargus:

Estimated live weight = 580,9 g

Estimated number = 61

$$\therefore \text{Estimated } \mu \text{ live weight} = \frac{580{,}9}{61} = 9{,}52 \text{ g}$$

Data collected in the present study provided a minimum estimate of numbers of each species in the faeces. This was multiplied by the estimated mean live weight for that species to give a final estimate of live weight of that species consumed.

Conversion factors are listed below in Table 2.

TABLE 2

Conversion factors for numbers of identified fish remains in spraints: live weight of fish species consumed

FISH SPECIES	ESTIMATED MEAN LIVE WEIGHT (g)
Chorisochismus dentex	12 849,0 ÷ 743 = 17,30
All Clinids	4,47
Cheilodactylus fasciatus	12,19
Chirodactylus brachydactylus	9,03
Acanthistius sebastoides	35,30
Diplodon sargus	9,52
Caffrogobius caffer	2,88
Sarpa salpa	13,60

The estimated live weights for Lithognathus mormyrus and Sparodon durbanensis could also have been calculated. However the live weight estimate for both these species in van der Zee (1979) was based on very small samples. If a mean live weight estimate had been calculated it would have been based on a sample of only seven Sparodon durbanensis and five Lithognathus mormyrus individuals. These two species were included in the unidentified pisces category for the calculation of estimated live weight. The contribution to estimated live weight would anyway have been very small (less than 0,5%).

The live weight estimate of unidentified Pisces was calculated using the minimum estimates of numbers of all identified and unidentified species. Thus for any given sample of spraints the estimated live weight of unidentified Pisces was calculated using the following formula:

$$L = \frac{U}{I + U} \times T$$

where L = estimated live weight of unidentified Pisces;

U = estimated number of unidentified Pisces.

I = estimated number of identified Pisces.

T = estimated live weight of all fish.

The value of T was estimated by applying the conversion factor listed in Table 1, to the weight of all fish remains in spraints.

As the only hard parts of octopus in spraints are the beaks, which constitute a tiny proportion of the total live weight, a conversion factor based on numbers rather than weight of prey remains had to be used to estimate live weight of octopus taken.

This was taken from Table 16 of van der Zee (1979) in which the estimated live weight of approximately 295 octopus taken by otters is given as 40 769,0 g. This gives a mean live weight estimate for individual octopuses of:

$$\frac{40\ 769,0}{295} = 138,2 \text{ g} \approx 138,0 \text{ g}$$

This estimate is used in the final analysis of estimated live weights of all prey species taken (Table 9).

All these conversion factors depend to a greater or lesser extent on the frequency distribution of size classes of each prey species being unchanged since van der Zee's work in 1977 and 1978. Later, results are presented to show that this is the case with two of the most important prey species: Plagusia chabrus and Chorisochismus dentex. For the purposes of this analysis it is assumed that it is also true for the remaining prey species.

In the final analysis of percentage live weights of all prey species there are two available estimates for the live weight of all fish species. One estimate is provided by using the conversion factor listed in Table 1, the other estimate by summing the estimated live weights for the identified fish species and the single estimate for unidentified pisces live weight. The problem now arises: which estimate should be used.

The estimate selected is that given by the Table 1 conversion factor. This conversion factor is the mean of five conversion factors calculated for five species of fish by van der Zee (1979). The species were Chlorisochismus dentex, Clinus cottoides, Chirodactylus brachydactylus, Sparodon durbanensis and Diplodus sargus.

There are two reasons for this selection. The first is that the estimate of live weight of all species obtained by summing the estimated live weights of individual species will tend to be an underestimate. This is because the numbers from which these live weights are calculated are minimum estimates. The estimate of numbers of a species was based almost entirely on the presence of identifiable premaxillae in the scats. The small size of these bones made detection of all those present very difficult and the fragility of the bones resulted in fragments that would not be recognised as premaxillae. Matching left and right premaxillae originating from the same spraint were assumed to be from the same fish, an assumption which ruled out any possibility of overestimation.

The second reason for using a live weight estimate based on the Table 1 conversion factor is that the Table 2 conversion factors are likely to be less accurate. The Table 1 conversion factor, estimating live weight of all fish caught from live weight of all fish remains, is based on values from van der Zee (1979) obtained by weighing the intact fish, boiling it to remove soft parts and then weighing the remaining hard parts. In contrast the Table 2 conversion factors were obtained by dividing estimated live weights of a species by estimated numbers of that species, the figures again taken from van der Zee (1979).

Thus the Table 1 conversion factor is used to obtain the estimate of live weight for <u>all</u> fish species. The Table 2 conversion factor is used to obtain live weight estimates of individual species. The latter figures are transformed into percentage of total fish live weight, obtained by summing the estimated live weights of each species and dividing by the total of these live weights. These percentages are then applied to the live weight of all fish caught, estimated from the weight of all fish remains and the Table 1 conversion factor. Thus it is hoped to combine the best available estimate of absolute biomass of all fish species caught with the only available estimate of proportions of each species taken. The final estimates of live weight of each fish species expressed as a percentage of the live weight of all prey taken, are shown in Table 9.

It was not possible to estimate the numbers of species taken directly from the weight of recognisable hard parts because less than half the bones found in spraints were identifiable to species level. This necessitated the rather complex procedure described above, to combine the best available estimates of total fish biomass and numbers of each species taken.

TRAPPING

Trapping was necessary for the remaining techniques employed in the study, all of which involved marking.

Standard caracal traps were used in the present study as they had been proved effective by van der Zee (1979).

Two traps were loaned by the Cape Provincial Administration Division of Nature Conservation for the duration of the study. Both traps had single doors activated by a treadle covering the entire rear half of the trap. Dimensions of the traps were 120 cm x 60 cm x 60 cm.

Traps were set on a total of 102 trap nights at known holts or spraint sites. Fish were used as bait, most commonly dageraad (*Chrysoblephus cristiceps*) or red steenbras (*Dentex rupestris*), but also Red Roman (*Chrysoblephus laticeps*), silverfish (*Argyrozona argyrozona*) and once a rock cod (Serranidae). As large a fish as possible was used as this undoubtedly gave the best results. Prior to setting the trap the mesh floor and treadle were covered with the local substrate (sand, soil, leaves etc.) and the trap itself rubbed down with the local vegetation, usually the odiferous curry bush, *Helichrysum maritimum*, in order to mask human scent.

Traps were set in the late afternoon or early evening and checked the next morning. Apart from otters, genets (*Genetta tigrina*) and water mongooses (*Atilax paludinosus*) often entered the trap to steal the bait. On a few occasions genets triggered the trap but escaped.

Captured otters were pinned into a corner of the trap using poles slid through the mesh sides. Each otter was immobilised with a combination of ketamine hydrochloride (Ketalar: Parke-Davies Laboratories, Isando) and acetopromazine (Parke-Davies Laboratories, Isando). The tranquillizer acetopromazine was used to combat the minor muscular convulsions often associated with the use of Ketalar alone. This was the combination of drugs previously used to good effect on *Aonyx* by van der Zee (1979).

The drug and tranquillizer were delivered simultaneously as an intramuscular injection to the thigh using a 2,5 cm^3 syringe. Body mass was estimated prior to injection and on the basis of this estimate a dose of 10 mg / kg body weight of ketamine hydrochloride and 1 mg / kg body weight of acetopromazine were used. Ketamine was usually administered at a concentration of 125 mg/ml and acetopromazine at a concentration of 10 mg/ml.

If the animal became intractable during handling boosters were administered usually of 30-35 mg of Ketalar and 2-3 mg of acetopromazine per otter. Response of the otters to these drugs varied considerably but no problems were encountered in the course of their use.

Depending on the trap site and marking technique to be used the animal was either processed in situ and kept in the trap until it recovered or removed to the laboratory at Stormsriver for processing. Animals receiving only ear tags, dye marking or shave marking were released the same day, as were two of the three otters receiving intramuscular injections of radioactive zinc chloride(^{65}ZnCl) [x].
Six otters receiving radio implants were held for a four to six day convalescence after the operation. The third otter receiving an intramuscular injection of ^{65}ZnCl was held for six days to monitor excretion of the radio-isotope.

These otters were held in a small enclosure (approximately 3 m x 2 m) built for the purpose at Stormsriver.

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[x] Amersham Laboratories, Amersham, England

MARKING

All animals were weighed and measured (Table 13) at capture, with the exception of the female caught at Nature's Valley. Teeth and pelage were examined to obtain a rough estimate of age and ectoparasites were collected.

Van der Zee (1979) employed a variety of techniques to mark *Aonyx*, two of which gave unsatisfactory results (large coloured plastic ear tags and freeze branding) and consequently were not utilized in the present study.

All twelve otters captured in the course of the study received at least one small (approximately 6 mm x 2 mm) aluminium numbered tag. These tags were only visible at close range in the field. However they were the only tags that remained attached for any length of time (one tag was still attached after 14 months) and provided certain identification of recaptures. Since tags were lost by some animals, the last seven animals caught were double-tagged with one marker in each ear.

Dayglo orange plastic "spaghetti" ear tags were used initially but these tags pulled out within a few weeks and their use was discontinued when double-marking with the aluminium tags was introduced.

Serious problems were encountered in marking otters for field recognition. As already noted, the "spaghetti" tags which were far more visible than aluminium tags and were available in a variety of colours to aid recognition, were soon lost. Three animals were marked with a red dye, Malathion Red (Ciba-Geigy (Pty) Ltd., Isando) that had been used with some success on Cape gannets, *Morus capensis*.

Unfortunately dilution of the dye was seen as soon as the marked animal entered the water after release. Despite notices asking tourists at the rest camp to report sightings of marked otters, no re-sightings were obtained. The technique was discontinued when re-capture of one of the three animals marked in this way revealed not a trace of the dye.

Picric acid was not used due to its toxicity. Otters groom regularly and ingestion of picric acid with attendant serious (even lethal) consequences was a possibility.

Near the end of the study two animals were marked by shaving a small patch of fur, approximately 10 cm^2 in extent, on the rump. Using different combinations of shaved patches on either haunch it would have been possible to individually mark several animals for field recognition. Unfortunately this marking technique is only temporary, such shaved patches remaining visible for at most six weeks. However if regular re-capture is possible, which appears to be the case with some animals, the otter can be re-marked. Even a mark which lasts for only six weeks can provide valuable data when an intensive radio-tracking study is being carried out on a limited section of coast.

Recaptures of marked animals yielded data on the age and status (resident or transient) of the otters. Trapping in general also provided some data on social organization but is not regarded as giving a reliable estimate of sex ratio as there is evidence to suggest that females may be more trap-shy than males.

POPULATION ESTIMATE

As is the case with most carnivores, the methods routinely used for estimating numbers were not readily applicable. Direct counting or sampling methods will not suffice due to the shy and elusive habits of Aonyx. Mark and recapture techniques are ruled out due to individual differences in trappability and non-random movement of the species.

Trapping gave some indication of population density and an estimate could be made on the basis of a number of assumptions. Thus if one assumes that: (i) after a prolonged trapping programme on one section of coast all the resident otters have been caught; (ii) home range sizes determined for this section of coast are applicable to the rest of the park, and; (iii) population density on the 58,5 km of coastline is not subject to significant variation, then one can arrive at an estimate of population size for the whole park. Given that these three assumptions are untested such an estimate would not be reliable enough as a basis for management recommendations.

The technique used to estimate the numbers of Aonyx on the Tsitsikama coast was first used by Kruuk, Gorman & Parish (1980) on the European badger, Meles meles.

The technique involves one or more animals, each receiving an intramuscular injection of the radio-isotope ^{65}Zn. In the present study the technique was first applied using the radio-isotope ^{51}Cr (one otter only). The experiment was later repeated with ^{65}Zn (three otters injected). The emission characteristics of the two isotopes used are shown overleaf in Table 3.

ISOTOPE	HALF-LIFE (DAYS)	MODE OF DECAY	µ ENERGY β MeV	ENERGY γ MeV
^{51}Cr	27.8	γ , κ	0,01	0,323
^{65}Zn	245	β+, γ, κ	0,10	1,11

TABLE 3 Emission characteristics of two radio isotopes used for radioactive labelling of Aonyx capensis in the Tsitsikama Coastal National Park

Three of the otters used in this experiment were captured and released at the mouth of the Geelhoutbos, west of Stormsriver. The remaining animal (injected with ^{65}Zn) was captured and released just west of Gammelbaai near the eastern boundary of the park. The implications of and reasoning behind this methodology are discussed later.

The ^{51}Cr was administered in a solution of $^{51}CrCl$ in 0,1 M HCl at a concentration of 100µCi/ml. The ^{65}Zn was administered in a solution of $^{65}ZnCl$ in 0,1 M HCl at a concentration of 100µCi/ml. The dosage of both isotopes was calculated on the basis of the 10µCi/kg body mass, used by Kruuk et al. (1980) for the badgers. All four animals were injected in the haunch.
The first three animals injected (one with ^{51}Cr and two with ^{65}Zn) were released immediately. The fourth otter, injected with ^{65}Zn, was kept in the convalescence enclosure for six days to monitor excretion of the ^{65}Zn.

Kruuk et al. (1980) used this technique in conjunction with radio-tracking and in the present study the first animal injected with ^{51}Cr, Naffer, also received a radio-implant. Unfortunately none of the remaining three injected with ^{65}Zn received a transmitter as there were none available at the time. Fitting radio transmitters enables death or migration to be detected.

The coast was cleaned of all faeces immediately after release of the labelled animal, to ensure that only faeces deposited after the marked individual was returned to its range were collected.

Detection of radio-activity in faeces was initially attempted in the field with a hand-held geiger counter, the Eberline Model E-120 (Scitec (Pty) Ltd, Sandton). When this proved unsuccessful all the faeces on a section of coast were collected, usually on more than one occasion, for reading in a more accurate γ counter.

Radio-active decay in the faeces collected after the release of the first otter, injected with ^{51}Cr, was measured solely on a Wilj, Sequential multi-isotope γ counter, model 2001-S (Sci-tec (Pty) Ltd., Sandton), at the University of Port Elizabeth. Radio-active decay in faeces collected after the release of the remaining three otters, all injected with ^{65}Zn, was measured on a Beckman γ 8000 counter (Laboratory & Scientific Equipment, Sandringham) in the laboratory. The count programme used entailed a five minute count for each sample, with a maximum of error of 0,5%, no rejection of background samples and a fully open window.

The estimate of population size in a study area is obtained by using the following formula:

$$G = I \times \frac{N}{n+}$$

where G = group size,

I = the number of individuals labelled,

N = total number of faeces collected

and n+ = the number of faeces which are labelled.

A statistically calculated threshold (Kruuk pers. comm.) was used to separate non-labelled and labelled spraints. The employment of a statistical threshold was necessitated by the absence of a clearly defined break between the γ counts of labelled and non-labelled spraints (Fig. 10). In the two samples (counted on two different counters, both Beckman γ 8000 models) a batch of spraints with the lowest γ counts, was extracted from the remainder of the sample. The γ counts of this batch apparently conformed to a normal distribution, a fact that was confirmed by a statistical test (see results). Variation in background radiation is known to be normally distributed and hence this batch of spraints was assumed to be the non-labelled fraction of the sample.

The exact threshold between labelled and non-labelled spraints was taken as the mean of the normally distributed γ counts plus 1,96 standard deviations. Details of the calculation of this threshold can be found in the results in Table 15 and Fig. 10 .

A threshold of the mean background count plus 1,96 standard deviations creates a threshold with confidence limits of 2,5%. It was not felt that higher confidence limits could be applied for this technique. Raising the confidence limits to 0,1% (mean + 3,09 standard deviations) would increase the likelihood of identifying labelled spraints as non-labelled spraints, thus over-estimating population size (Kruuk, pers. comm.). Such a change in confidence limits would have increased the population estimate by 5-10%. If conclusions on the effectiveness of present levels protection or future management of the species are to be made on the basis of these results, a slight underestimate of population size is preferable to slight overestimate of population size.

As only one adult female was marked with ^{65}Zn in the study area at the eastern extremity of the park, this technique also provided some data on home range size of females (not available from the radio-tracking data) and patterns of female home range utilization. It also proved possible to make some tentative conclusions on the behaviour of females with regard to social organization on the basis of the distribution of radio-active spraints between the Lottering River and Rietmondjie.

RADIO-TRACKING

The low population density characteristic of carnivores, the elusiveness of otters, their nocturnal habits and the rigours of the Tsitsikama terrain would provide insuperable problems for the worker trying to obtain data by direct observation. During a 15-month study van der Zee (1979) saw otters on only 35 occasions. During the present study conducted over a period of 17 months only 21 incidental sightings (i.e. without the use of radio-tracking) of Aonyx were obtained.

Such sightings provide only fragmentary evidence on the behaviour and ecology of a species, especially when the animals are not individually recognisable. The problems encountered in attempting to mark these animals for field recognition have been mentioned (above). The present study was designed to overcome the problems encountered by van der Zee and as such was based largely on radio-tracking. Radio-tracking not only enhances the researcher's ability to locate the animal, but also by using radios transmitting on different frequencies provides a reliable method of identification.

The radio-tracking equipment, with the exception of the 4-element Yagi antenna used, was supplied by the AVM Instrument Co. (6575 Trinity Court, Dublin, California 94566). The receiver used was an LA12. A total of five SB-2 transmitters, transmitting on different frequencies, namely 150.950, 150.900, 150.850, 151.025 and 151.608 MHz, were used in six different animals. One transmitter was re-used after recovery from the body of the second otter to be radio-tracked, which had died approximately two weeks after release.

All the radios were implanted in the peritoneal cavity of the otter. The circumference of the otter's neck is wider than the head so that collars can be slipped off. Harness design presents formidable problems in an animal as lithe and dexterous as *Aonyx*. Harnesses suitable for use with the European otter *Lutra lutra* have only recently been designed (Dunstone,* *pers. comm.*). A harness fitted to a tame Cape clawless otter owned by Dr G.A. Robinson was removed by the animal in less than two minutes (Robinson, *pers. comm.*). Given the manual dexterity of *Aonyx* it seems likely that an effective harness will prove even more difficult to design for this species than for other lutrines which have more extensive webbing and no semi-opposable first digit.

A technique for the intraperitoneal implantation of a radio-transmitter in the North American river otter, *Lutra canadensis*, was developed by Melquist & Hornocker (1979). These workers used two different sizes of transmitter, one weighing 130g and the other 65g. They obtained satisfactory results with both transmitters and as *Aonyx* is a larger animal than *Lutra canadensis* implantation of radios of a similar size was deemed feasible.

In the present study the five transmitters used were the AVM SB-2 model with either two Hg 601 mercury cells (4 transmitters) or two 2/3 A lithium cells (one transmitter). Both types of implant had approximate dimensions of 65 mm x 25 mm (diameter) and weighed 70 g. The aerial was a small loop incorporated within the dental acrylic coating of the implant.

All six implantations were performed by Dr A.H. Reitz B.Sc. B.V.Sc. at his surgery in Knysna. The animals were conveyed to Knysna in a drugged state in either a wood and wire mesh carrying trap or a caracal

*Dr N. Dunstone, Dept of Zoology, University of Durham, South Road, Durham DH1 3LD, England trap. Five of the six otters were conveyed directly from the trap site to Knysna and underwent surgery on the day of capture. The sixth was taken for surgery on the day following capture after an abortive but prolonged escape attempt ruled out implantation on the first day.

Dr Reitz made some minor modifications to the procedure employed by Melquist & Hornocker (1979) on Lutra canadensis. For the premedical anaesthesia ketamine hydrochloride (Ketalar: Parke-Davis Laboratories, Isando) was used at a dose rate of ± 10 mg/kg body weight, in conjunction with acetopromazine (Parke-Davis Laboratories, Isando) at a dose rate of 1 mg / kg body weight. The otter was shaved over a paralumbar area of approximately 15 cm x 10 cm. A ± 6 cm incision is made through the skin followed by the three muscle layers and peritoneum. The radio, which had been immersed for ± 20 minutes in a 0,5% solution of Povidine Iodine for sterilization, was then inserted through the incision into the peritoneal cavity.

In the first two animals receiving the implant, both adult males, the transmitter was left to "float free" in the peritoneal cavity. However the smaller of these two males was found dead three weeks after his release and there was some evidence to suggest that the unattached transmitter may have been a contributory factor. As a result the remaining four transmitters were attached to the pelvis to limit movement within the peritoneal cavity. Attachment was achieved by drilling a hole through the wing of the ilium and threading a strong monofilament nylon thread through it (two implants). Alternatively the monofilament nylon was simply looped through a section of the fascia using a needle (two implants). The monofilament was attached to the radio implant by turns through the loop antenna. The antenna was encased in dental acrylic endowing its loop antenna with sufficient mechanical strength for such an attachment.

After implantation the incision was closed with simple interrupted sutures through the muscle, peritoneum and skin. Catgut was used for the sutures in the peritoneum and muscle layers while a nylon monofilament was used for the skin sutures.

The operation was usually completed within 20 minutes and the animal transferred from operating table to carrying trap while still under anaesthetic. On arrival at Tsitsikama the animal was placed in a 3 m x 2 m holding enclosure for a period of convalescence.

Five males and one female received radio-implants. The heaviest animal was a 17,8 kg male and the lightest an 11,0 kg female (weights and measurements of all otters trapped in the course of the study are given in Table 13). Thus the 70 g radio transmitter represented no more than 0,6% of body weight in the smallest Aonyx implanted and less than 0,4% of body weight of the largest animal implanted. This is well below the usual limits set for the weight of biotelemetry units, namely 3-5% of body weight.

After a five to six day convalescence the animals were cornered in the holding enclosure using poles, wire mesh and on three occasions a sack, drugged and transferred to the carrying trap. At this point they were carefully examined to ensure that the implantation wound was healing properly. Ectoparasites picked up in the holding enclosure were removed. The second animal to be radio tracked, a 13,0 kg male, received an intramuscular injection of 130 µCi of the radio-isotope Chromium (^{51}Cr) at this stage (see Population estimate method).

Once it was ascertained that the animal was healthy, it was transported to its capture site to await recovery from the drugs (4-6 hours after administration). Radio-tracking began as soon as the animal was released, the otter being monitored intensively in the first few days after release to establish whether or not the animal was resident in the area.

The basic receiving equipment employed during the study consisted of the LA12 receiver and a 4-element Yagi constructed in the Zoology Department, University of Pretoria. The antenna was constructed with dimensions for optimal reception of frequencies between 146-154 MHz. Initially the four receiving elements were only pop-riveted to the main boom. However constant tracking in thick bush loosened the riveted elements reducing the performance of the antenna. Both antennae were later aluminium welded to maintain configuration for the final three months of radio-tracking. Aluminium welding also served to reduce the vulnerability of the antennae to breakages.

The five males were tracked for periods varying between 5 days and 73 days. Tracking was carried out in the months of June, September, October and December 1981 and January, June, July and August of 1982. Thus radio-tracking studies extended through only three seasons, namely winter, spring and summer.

The first two animals released were only tracked during the day. Night-tracking was initiated with the release of the third animal, Biggles, in October. Both the subsequent animals were night-tracked as it became apparent that _Aonyx_ is largely nocturnal in the Tsitsikama.

During the day radio-tracking was essentially predictive (Macdonald 1978) the signal being used to locate the animal and establish visual contact. Whenever visual contact was lost the radio was used to re-locate the animal.

Only two visuals were obtained at night in the course of the study as no night-vision or spot-lighting equipment was available. However an impression of the otter's activity at night could be gained from the behaviour of the radio signal. The animal's position was plotted by instantaneous triangulation in relation to known points on the coast. The otters were effectively moving in only one dimension - back and forth along a narrow strip of coast. This simplified the collection, analysis and interpretation of movement data amassed during night-tracking.

For the final analysis the known home ranges of the otters were divided into 500 m, straight-line distance sections (Fig. 18). The radio-tracking data provided estimates of time spent in a section and speed in the water through that section. For each complete foray, i.e. the period of activity between leaving and entering a holt, the displacement along the coast, average speed and length of foray in minutes were recorded (see Table 24). The length of the rest following each foray was recorded where possible, and the holt which was used.

Environmental factors included in the analysis were time of day, (recorded simply as day or night), sea temperature, tide state (recorded as low, high, rising or falling) and sea conditions where possible.

These results were subject to a comprehensive statistical analysis using both parametric and non-parametric statistics. The relationship of behavioural parameters to environmental conditions and other behavioural parameters were examined.

Home range utilization was assessed by scoring the presence of radio-tracked animal in a sector each time the animal was initially located in that sector or entered the sector in the course of radio-tracking. Thus if an animal backtracked to re-enter a previously occupied sector his presence there would be scored twice for that radio-track. Total time spent foraging in each sector in minutes was also recorded (Table 24). Home range utilisation was depicted as a histogram using the coast as the horizontal axis (Fig. 21).

Holt utilization was scored in a similar fashion on the entry of an animal to a holt. Total time spent in the holt during monitoring was also recorded (Table 22).

Comparative statistical analysis was performed on home range utilisation and holt utilisation data of individual otters, as well as between this utilisation data and the available quantified foraging behaviour.

The overall analysis was designed to elucidate any patterns in the movement and foraging behaviour of _Aonyx_, and where possible relate any such patterns to each other and to environmental conditions.

Parametric and non-parametric statistical tests were used, non-parametric tests being applied in most cases.

Only one parametric test, Pearson's correlation coefficient (Siegel, 1956) was used when large samples ($N \geqslant 30$) were being tested. The non-parametric tests used consisted of Kendall's (Siegel, 1956) and Spearman's (Siegel, 1956) rank correlation coefficients (the first for samples of $N \leqslant 10$ and the second for samples of $11 \leqslant N < 30$), various χ^2 tests (Siegel, 1956), the Fisher exact probability test (Siegel, 1956), the Mann-Whitney U test (Siegel, 1956) and the Kruskal-Wallis one way analysis of variance (Siegel, 1956).

Correlations between behavioural variables (e.g. foray duration and rest time, home range utilisation and foraging behaviour) and between behavioural variables and environmental conditions (e.g. foray duration and sea temperature, foray speed and sea conditions) were investigated.

Quantitative differences in nocturnal and diurnal behaviour were tested for significance. Most of the tests were applied to examine differences in behaviour of the same otter under different conditions. However tests of significance were also applied to behavioural data from different otters under the same conditions. Interpretation of these results was not straightforward as differences in behaviour may have been attributable to seasonality rather than individual variation.

RESULTS

COASTAL SURVEY

The occurrence of otter sign (tracks and spraints) on 6 km of coast between George se baai and Steilkop, is presented in Table 4. For each holt or spraint site the number of spraints and the number of times tracks were present is recorded. Only fresh sign was counted to avoid the possibility of scoring a set of tracks or a spraint more than once. The survey was conducted over a period of fourteen weeks. The distribution of sign is recorded for each month during this period with the dates of the first and last survey in that month. The location of the holts and spraint sites surveyed is indicated in Fig. 18.

TABLE 4

Occurrence of otter sign at different sites in the Tsitsikama Coastal National Park during a four-month period

Period		Boulder Gully	Holt 34	Holt 5	Holt 4	Goudgate Gully	Holt 1	Holt 12	Holt 6	Holt 10	Holt 7
3/2/81 to 28/2/81	Spraints	3	4	13	4	7	0	9	15	0	18
	Tracks	6	-	-	-	4	1	-	-	-	-
2/3/81 to 28/3/81	Spraints	12	0	5	18	3	0	3	5	0	12
	Tracks	3	-	-	-	5	0	-	-	-	-
4/4/81 to 19/4/81	Spraints	0	0	0	8	3	3	1	4	0	13
	Tracks	1	-	-	-	3	1	-	-	-	-
4/5/81 to 21/5/81	Spraints	17	0	9	1	2	5	4	10	16	21
	Tracks	4	-	-	-	4	1	-	-	-	-
3/2/81 to 21/5/81	Spraints	32	4	27	31	15	8	17	34	16	64
	Tracks	14	-	-	-	16	3	-	-	-	-

These results are compared with the home range utilisation data obtained during radio-tracking (Table 22, Fig. 30). The intermittent use of holts is discussed in relation to foraging strategy, in a later section.

Temporal variation in the utilisation of holts can only be assessed after the variations in length of the four surveys have been accounted for. The survey in February covered 26 days, in March 27 days, in April 16 days and in May 18 days. By dividing the number of spraints found at one location in a month (Table 4) by the number of days in the survey period for that month a figure for spraints per survey day is obtained. The temporal variation in the utilisation of four holts in this section is recorded graphically in Figure 5 .

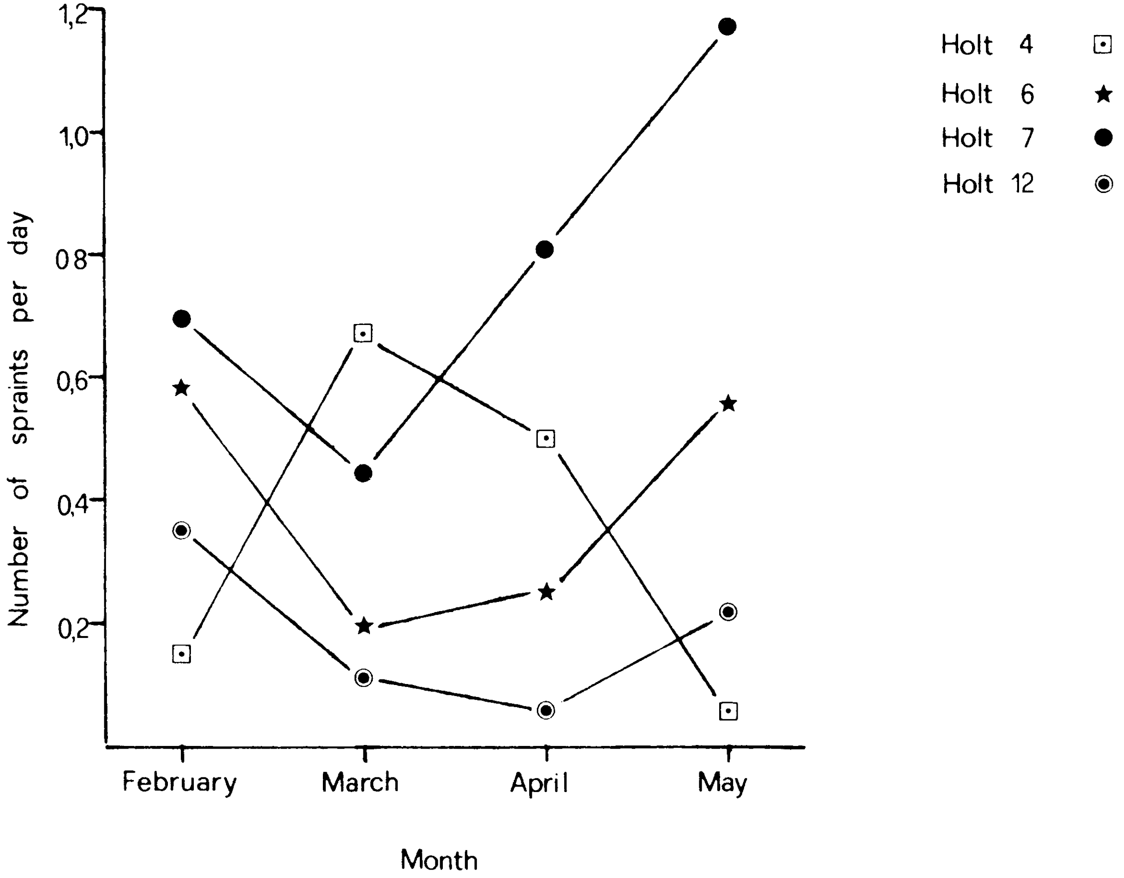
Though two coastal surveys were undertaken, only the results of the second are presented (Table 5 and Fig. 6). The coast was divided into sections, identified in table 5 , for the purpose of comparing holt and spraint densities. Rivers were used to demarcate the section boundaries.

In Table 6 sections of coast coinciding with particular study areas have been selected; for example this table includes the holt and spraint densities for Biggles' and Dougal's known home ranges.

Statistical analysis was applied to the spraint densities and holt densities recorded in Table 5. Spraint densities were significantly higher east of Stormsriver than west of Stormsriver (Mann-Whitney U-text, $U=4$, $n_1=5$, $n_2=6$, $P<0,05$). There was however no significant difference in the density of holts on either side of Stormsriver (Mann-Whitney U-test, $n_1=5$, $n_2=6$, $P>0,20$).

four different sites in the Tsitsikama Coastal

National Park



Number of spraints at holt 4 vs. total number at holts 6, 7 and 12.

Kendall's Rank Correlation Coefficient: N=4, S=6, p=0.042.

TABLE 5

Distribution of otter holts and spraints in the Tsitsikama Coastal National Park. Survey conducted in March 1982.

Section of coast	Length * S.L.D. (km)	Holts	Spraints	Holts/ km S.L.D.	Spraints/ km S.L.D.	Spraints/ holt
Nature's Valley - Bloukrans	7,2	7	155	0,97 $\frac{7}{7.2}$	21,5 155	22,1 $\frac{155}{7}$
Bloukrans - Witels	5	9	143	1,80	28,6	15,9
Witels - Lottering	3,2	7	143	2,19	44,7	20,4
Lottering - Elandsbos	3,0	7	152	2,33	50,7	21,7
Elandsbos - Kleinbos	4,3	10	210	2,33	48,8	21,0
Kleinbos - Stormsriver	8,4	15	409	1,79	48,7	27,3
Nature's Valley - Stormsriver	31,1	55	1212	1,77	39,0	22,0
Stormsriver - Langbos	6,6	15	378	2,27	57,3	25,2
Langbos - Sandrif	3,0	6	160	2,0	53,3	26,7
Sandrif - Elands	6,7	16	454	2,39	67,8	28,4
Elands - Jaftas	4,9	15	303	3,06	61,8	20,2
Jaftas - Groot (E)	6,1	13	265	2,13	43,4	20,4
Stormsriver - Groot (E)	27,3	65	1560	2,38	57,1	23,6
Grootrivier (W) - Grootrivier (E)	58,4	120	2772	2,05	47,5	22,9

*S.L.D. = straight line distance

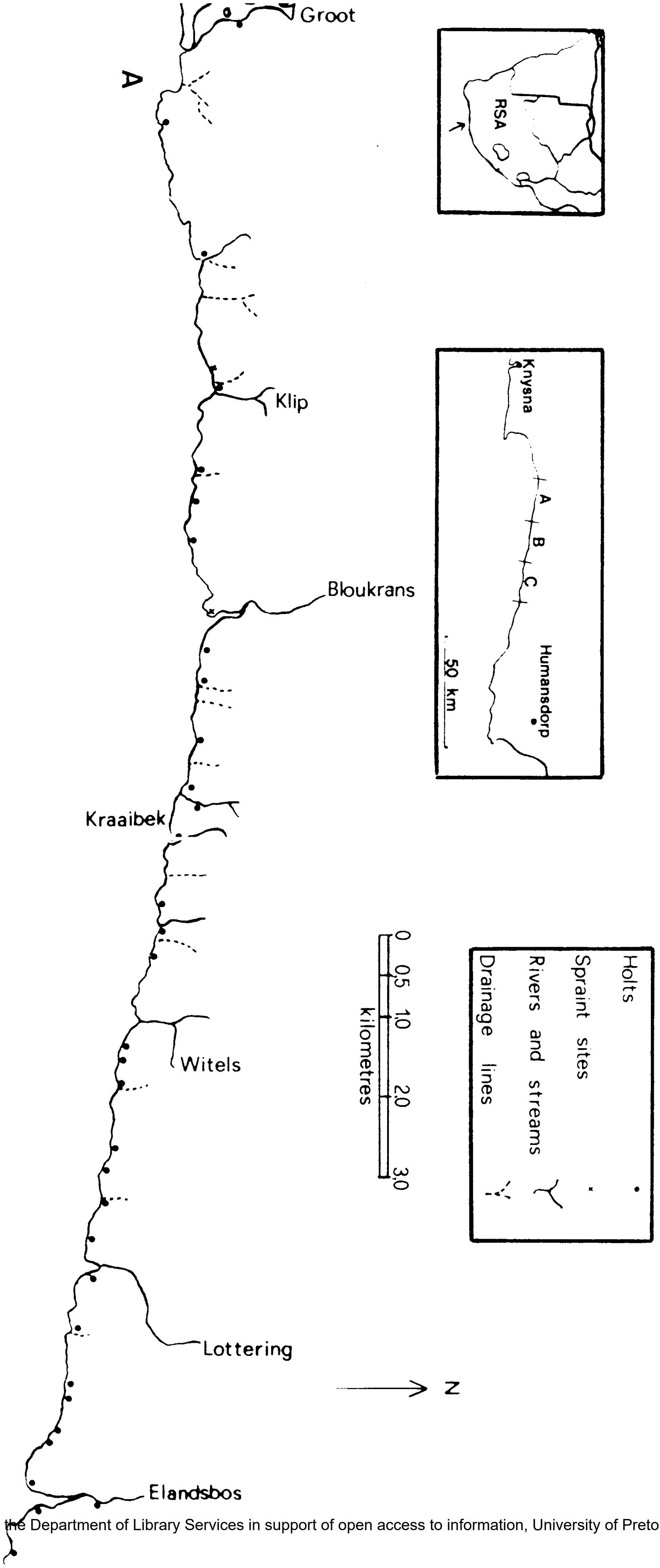

Groot
A
Klip
Bloukrans
Kraaibek
Witels
Lottering
Elandsbos
RSA
Knysna
A
B
C
Humansdorp
50 km
0
0,5
1,0
2,0
3,0
kilometres
Holts
Spraint sites
Rivers and streams
Drainage lines
N

TABLE 6

Distribution of otter holts and spraints in specific study areas in the Tsitsikama Coastal National Park. Survey conducted in March 1982.

	Section of coast	Length S.L.D. (km)	Holts	Spraints	Holts/ km	Spraints/ km	Spraints/ holt
BIGGLES' HOME RANGE	Bloukrans - Geelhoutbos	12,9	27	519	2,09 (2,1)	40,2 (40)	19,2
DOUGAL'S HOME RANGE	Geelhoutbos - Tommy Pedro	18,6	38	983	2,04 (2,0)	52,8	25,9
MAIN STUDY AREA	Kleinbos - Steilkop	10,3	19	488	1,84 (1,8)	47,4 (47)	25,6
COLLECTION AREAS FOR ^{65}Zn SPRAINTS	Elands - Groot (E)	11,0	27	568	2,45 (2,5)	51,6 (52)	21,0 (21)
	Elandsbos - Rietmondjie	4,8	20	472	2,04	48,2	23,6
REST CAMP	Underwater Trail - Mooibaai	2,0	2	65	1,00	32,5	32,5

There is a significant correlation between holt and spraint densities in the eleven sections of coast (Spearman's rank correlation coefficient: $r_s = +0{,}780$, $n = 11$, $P < 0{,}01$).

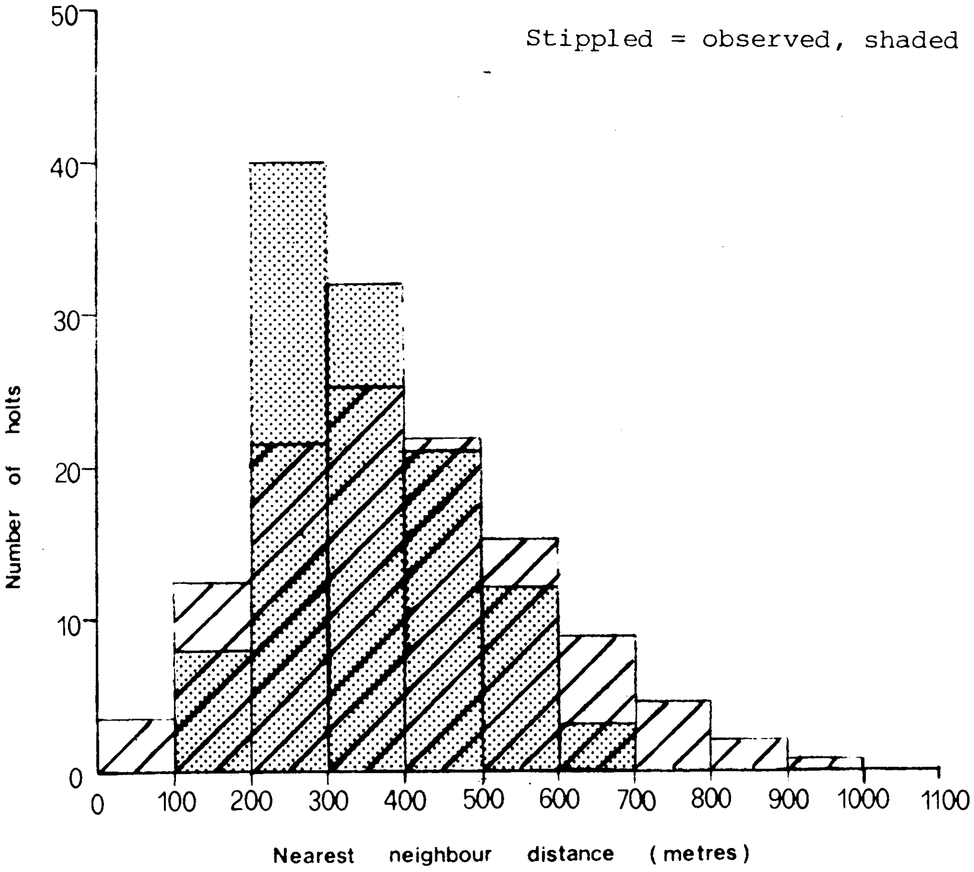
The holt and spraint densities recorded in Table 6 are included in the discussion of the results of radio-tracking studies and the ^{65}Zn population estimates performed in those areas.

The distribution of nearest neighbour distances between otter holts was examined. These nearest neighbour distances were measured from the map in Figure 6, for 116 holts between the Klip River in the west and the Groot River in the east. The four holts lying west of the Klip River were not included as the topography of this 4,3 km section of coast precluded a thorough survey. Furthermore this section was atypical of the remainder of the Tsitsikama coast, in that much of it consisted of sheer cliffs.

The nearest neighbour distances used were straight-line distances rather than the length of coastline between holts. The length of coastline was difficult to measure reliably and the method chosen here allows direct comparison with the data of Kruuk & Hewson (1978) on the spacing of holts in Lutra lutra.

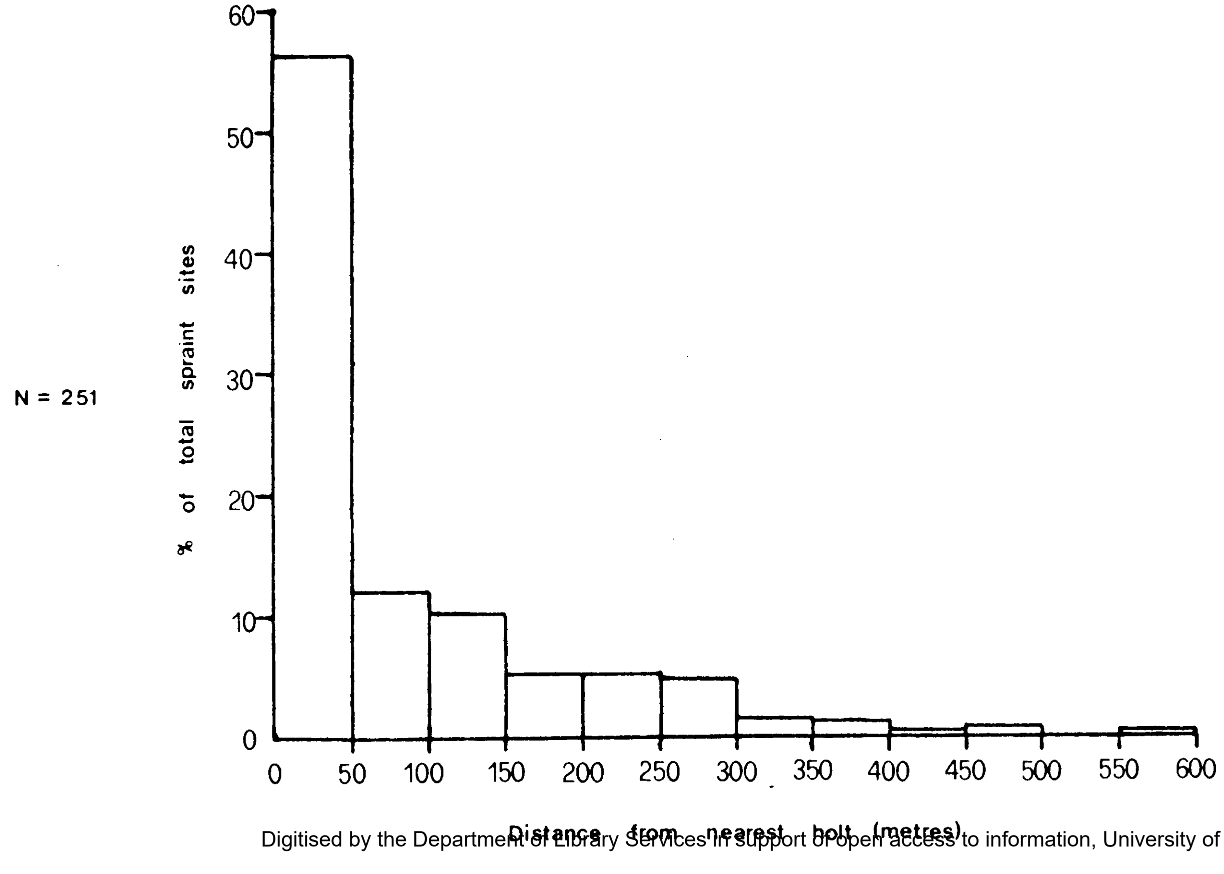
The frequency distributions of holt nearest neighbour distances and a hypothetical random distribution, generated by the Poisson expansion, are shown in Figure 7. The mean nearest neighbour distance was 348 m straight-line distance. The observed and random distribution of nearest neighbour distances differed significantly ($\chi^2 = 33{,}09$, 6 df, $P < 0{,}001$), the observed distribution exhibiting fewer closely spaced (0-200 m) and widely spaced (500-900 m) holts than the random distribution. Thus it would appear that there is a

Fig. 7 Nearest neighbour distances between 116 otter holts in the Tsitsikama Coastal National Park, March 1982



Stippled = observed, shaded = hypothetical rando

Fig. 8 Distance of spraint sites from nearest holt in the Tsitsikama Coastal National Park, March 1982



tendency towards even spacing of holts. As there was an abundance of suitable sites for holts it seems likely that there was a behavioural mechanism controlling this spatial arrangement.

Of the 2772 spraints recorded during the March 1982 coastal survey, 85,4% were within 50 m of a holt (a mean of 19,5 spraints per holt). The remaining 14,6% were deposited at irregular intervals. Of these 1,1% were deposited singly and 9,1% in groups of 2-10. Only seven regularly used spraint sites that were not in the immediate vicinity of a holt ("lavatories") were located during the survey (Fig. 6). These seven sites accounted for only 4,4% of the spraints located. It is probable that not all such spraint sites were located.

The distribution of all spraint sites, in relation to the holts, including those marked by only a single spraint, is illustrated in Figure 8. This refers only to those spraint sites in use at the time of the coastal survey in March 1982. The majority of spraint sites are within 50 m of a holt (56,2%). As 85,4% of all spraints lie within 50 m of a holt, it is clear that there are not only more sites close to holts, but that these sites are also more intensively used.

The observed spraint site distributions are later compared with those recorded by Kruuk & Hewson (1978) and Macdonald & Mason (1980) for coastal populations of Lutra lutra.

FEEDING ECOLOGY

Spraint samples from the home ranges of Biggles and Fat Freddy (Fig. 14) were compared (tables 7 & 8) to investigate spatial variation in dietary composition.

Table 7 compares the proportions of the four main categories of prey in 100 spraints collected between the Bloukrans and Geelhoutbos Rivers (Biggles' range) and 101 spraints collected between the Kleinbos River and Steilkop (Fat Freddy's range). These categories are the red rock crab, Plagusia chabrus, the brown rock crab, Cyclograpsis punctatus, all the fish species recorded in spraints and the common octopus, Octopus granulatus.

The estimated live weights presented in Table 7 were calculated using the conversion factors in Table 1 and the estimate of mean live weight of Octopus granulatus (page 20), all taken from van der Zee (1979).

Variation in the relative percentage frequency of the four prey categories between the Bloukrans-Geelhoutbos River and Kleinbos River - Steilkop study areas is not significant ($\chi^2 = 1{,}47$, 3 df, $P > 0{,}500$). There is however significant variation in the proportion of weighed remains of all fish species and the two crab species between the two areas ($\chi^2 = 53{,}85$, 2 df, $P < 0{,}001$). There is a higher proportion of crab remains from the Bloukrans-Geelhoutbos River stretch. This difference is reflected in the estimates of live weight consumed for all four categories, fish species contributing a significantly higher proportion and crab species a significantly lower proportion in the Bloukrans-Geelhoutbos River section ($\chi^2 = 63{,}31$, 3 df, $P < 0{,}001$).

TABLE 7

Composition of 201 spraints and estimated live weight of contributing prey of *Aonyx capensis* collected from two separate areas in the Tsitsikama Coastal National Park, March 1982

Sampled area	Prey	Occurrence in spraints	%age frequency	Relative %age frequency	Number of individuals	Weight prey remains (g)	%age weight of prey remains	Estimated live weight consumed * (g)
Bloukrans-Geelhoutbos n=100	*Plagusia chabrus*	91	91	35,7	-	731,4	66,2	3660
	Cyclograpsus punctatus	64	64	25,1	-	127,4	11,5	640
	All fish spp.	88	88	34,5	-	246,2	22,3	4600
	Octopus granulatus	12	12	4,7	12	-	-	1660
	TOTALS	255				1105,0		10560
Kleinbos-Steilkop n=101	*Plagusia chabrus*	91	90,1	36,7	-	792,8	70,2	3960
	Cyclograpsus punctatus	70	69,3	28,2	-	203,8	18,0	1020
	All fish spp.	79	78,2	31,9	-	132,7	11,8	2460
	Octopus granulatus	8	7,9	3,2	9	-	-	1240
	TOTALS	248				1129,3		8680

*To the nearest 10g

Table 8 presents the occurrence of the most important species of fish in the diet of Aonyx including estimates of live weight of each species consumed as a percentage. Live weights were calculated from the number of individuals of each species recorded in the spraints using the conversion factors (mean live weight estimates from van der Zee, 1979) listed in Table 2 .

In Table 8 relative percentage frequency of each fish species was calculated as the number of scores of that species in the spraints as a percentage of the total number of scores of all species (fish, crabs and octopus) found in the spraints. Percentage live weight consumed of each fish species was calculated as a percentage of the total estimated live weight consumed of all identified fish species.

Spraints collected from the Bloukrans-Geelhoutbos River section contained a lower proportion of Chorisochismus dentex and higher proportions of the Cheilodactylus fasciatus, Chirodactylus brachydactylus and clinids than spraints collected from the Kleinbos River - Steilkop section ($\chi^2 = 26,78$, 3 df, $P < 0,001$).

The percentage live weight estimates of all prey species recorded in the 201 spraints, with the exception of five fish species, are presented for the two sample areas in Table 9 . Though fragments of bones of Pomatomus saltator, Sparodon durbanensis, Lithognathus mormyrus, Epinephalus andersoni and Diplodus trifasciatus were identified in some of the 201 spraints, no live weight estimates were calculated. This was either because no estimate of mean live weight of individuals was available or because this mean, calculated by van der Zee (1979) was based on too small a sample to be reliable. These five species are included in the live weight estimated for unidentified Pisces.

TABLE 8

Occurrence of identified fish in 201 spraints collected from two separate areas in the Tsitsikama Coastal National Park, March 1982

Sample area	Prey species	Occurrence No. of spraints	%age frequency	Relative %age frequency	No. of individuals	%age of identified fish live weight consumed
Bloukrans - Geelhoutbos n=100	*Chorisochismus dentex*	46	46	12,8	81	41,1
	Cheilodactylus fasciatus	36	36	10,0	74	20,2
	Clinids	61	61	17,0	153	26,5
	Chirodactylus brachydactylus	18	18	5,0	23	6,1
	Caffrogobius caffer	5	5	1,4	9	0,8
	Acanthistius sebastoides	3	3	0,8	3	3,1
	Diplodon sargus	5	5	1,4	5	1,4
	Sarpa salpa	2	2	0,6	2	0,8
	TOTALS	176			350	100,0
Kleinbos - Steilkop n=101	*Chorisochismus dentex*	45	44,5	14,6	73	58,0
	Cheilodactylus fasciatus	15	14,9	4,9	19	10,6
	Clinids	34	33,7	11,1	63	13,0
	Chirodactylus brachydactylus	4	4,0	1,3	4	1,7
	Caffrogobius caffer	4	4,0	1,3	5	0,7
	Acanthistius sebastoides	5	5,0	1,6	6	9,7
	Diplodon sargus	9	8,9	2,9	13	5,7
	Sarpa salpa	1	1,0	0,3	1	0,6
	TOTALS	117			184	100,0

TABLE 9

Estimated percentage live masses of prey species in the diet of *Aonyx capensis* in two areas in the Tsitsikama Coastal National Park, March 1982

Species	Sampled areas	
	Kleinbos River - Steilkop	Bloukrans River - Geelhoutbos River
Plagusia chabrus	45,6	34,7
Cyclograpsus punctatus	11,7	6,0
Octopus granulatus	14,3	15,7
Chorisochismus dentex	15,2	17,0
Clinids	3,4	8,4
Cheilodactylus fasciatus	2,8	11,0
Chirodactylus brachydactylus	0,4	2,5
Caffrogobius caffer	0,2	0,3
Diplodon sargus	1,5	0,6
Acanthistius sebastoides	2,5	1,3
Sarpa salpa	0,2	0,3
Unidentified Pisces	2,3	2,4
All Pisces	28,4	43,6
Sample sizes	n=101	n=100

Twenty spraints collected at holts at least 500 m upriver from the mouths of the Bloukrans, Lottering and Elandsbos are not included in this detailed analysis. These were the first 20 spraints to be examined and as such were analysed less accurately than the 201 spraints collected on the coast. However it is worth noting that none of the 20 spraints collected in the three rivers were found to contain remains of freshwater organisms.

Using linear regressions calculated by van der Zee (1979) it was possible to estimate the size of individuals of two prey species from indigestible hard parts found in the spraints. The carapace width of the red rock crab, *Plagusia chabrus*, could be calculated from the intact chela or finger length, van der Zee (1979). The length of the rocksucker, *Chorisochismus dentex*, one of the fish preyed upon by *Aonyx*, can be estimated from the length of the premaxilla. The results are presented in Table 10 .

TABLE 10

Frequency distributions of size classes of *Plagusia chabrus* and *Chorisochismus dentex* estimated from hard parts collected in spraints of *Aonyx capensis* from two separate areas in the Tsitsikama Coastal National Park, March 1982

	Carapace width of *Plagusia chabrus* (mm)								
Sampled area	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	Sample size
Bloukrans R. - Geelhoutbos River	0	8	19	17	17	4	6	0	71
Kleinbos R. - Steilkop	0	4	10	11	14	1	3	0	43

	Length of *Chorisochismus dentex* (mm)									
Sampled area	10-30	30-50	50-70	70-90	90-110	110-130	130-150	150-170	170-190	Sample size
Bloukrans R. - Geelhoutbos River	0	2	12	10	15	5	0	0	0	44
Kleinbos R. - Steilkop	0	1	15	13	8	3	1	1	0	42

There is no significant variation in the frequency distribution of size classes of *Plagusia chabrus* (χ^2 = 1,44, 2 df, P > 0,500) or of *Chorisochismus dentex* (χ^2 = 2,56, 3 df, P > 0,10) between the two areas.

Data collected in the present study were compared with data collected by van der Zee (1979) in March 1977 and March 1978. Van der Zee (1979) collected from a 5 km stretch of coast contained within the Kleinbos River - Steilkop section, so data collected from this section in the present study were used in the comparison. There was no significant temporal variation in the frequency distribution of size classes of either prey species in the spraints of *Aonyx* (*Chorisochismus dentex*; $\chi^2 = 1,74$, 3 df, $P > 0,50$ and *Plagusia chabrus*; $\chi^2 = 1,61$, 3 df, $P > 0,50$).

The proportions of *Chorisochismus dentex*, *Cheilodactylus fasciatus*, *Chirodactylus brachydactylus* and members of the Clinidae, expressed as numbers of individuals of each taxa found in the spraints were also tested for temporal variation using data from van der Zee (1979) and the present study. Proportions of *Chorisochismus dentex* and the Clinidae showed little temporal variation but there was a significantly higher proportion of *Cheilodactylus fasciatus* and a significantly lower proportion of *Chirodactylus brachydactylus* in the sample collected during the present study ($\chi^2 = 80,47$, 3 df, $P < 0,001$).

CALORIFIC VALUE OF PREY SPECIES

Calorific values were determined by bomb calorimetry for three of the prey species of *Aonyx*. These were the brown rock crab, *Cyclograpsus punctatus* (10,7 KJ g^{-1} dry mass), and two fish species, *Clinus cottoides* (22,0 KJ g^{-1} dry mass), and *Cheilodactylus fasciatus* (21,3 KJ g^{-1} dry mass). Unfortunately there are no wet mass : dry mass ratios available for these three species.

TRAPPING

The results of the trapping programme, conducted at ten separate sites, eight of them within the Park and two outside the Park, are shown in Tables 11, 12 & 13. Location of the trap sites is shown on the map in Fig. 6. The two trap sites outside the Park, Blue Rocks and Salt River estuary, were located in de Vasselot Nature Reserve between 2½ and 3 km west of the western boundary of the Park and are not shown in this figure.

Table 11 gives the trap rate as percentage success for individual sites. Table 12 presents the trap rate for groups of sites, classified according to their position in relation to the rest camp and the Park boundary.

TABLE 11

Trapping success for <u>Aonyx capensis</u> at different sites in the Tsitsikama Coastal National Park, May 1981-- August 1982

Trap site No.	Trap site	Trap nights	No. of captures	% success
1	Holt 1	26	4	15,4
2	Goudgate Gully	35	3	8,6
3	Holt 4	1	0	0
4	Holt 5	9	3	33,3
5	Geelhoutbos - holt 18	6	4	66,7
6	Geelhoutbos - stream holt	1	0	0
7	Holt 500 m west of Gammelbaai	2	1	50,0
8	Holt 500 m west of holt 37	6	1	16,7
9	Blue Rocks	8	0	0
10	Salt River Estuary	8	1	12,5
	All sites	102	17	16,7

TABLE 12

Comparison of trapping success for <u>Aonyx capensis</u> in different areas of the Tsitsikama Coastal National Park, May 1981 - August 1982

Trap site	Trap nights	No. of captures	% success
Rest camp and immediate vicinity	62	7	11,3
Remainder of National Park	24	9	37,5
Outside Park boundaries	16	1	6,3
Inside Park boundaries	86	16	18,6

Table 13 lists the sex, dimensions and weight of the twelve otters trapped.

TABLE 13

Measurements of <u>Aonyx capensis</u> trapped in the Tsitsikama Coastal National Park, May 1981 - August 1982

Sex	Number (name) of otter	Length (mm) head & body	Length (mm) tail	Length (mm) Total	Length (mm) Hindfoot	Weight (kg)
Male (A)	1, Oleg	160 + 675	480	1315	162	15,5
Male (A)	2, Eric	180 + 665	500	1345	170	17,7
Male (A)	3, Naffer	172 + 598	530	1300	160	13,0
Male (A)	4, Biggles	180 + 620	510	1310	160	13,8
Male (A)	5, Fat Freddy	165 + 705	510	1380	160	13,5
Male (A)	7, Dougal	155 + 685	445	1285	155	14,2
Female (A)	6	-	-	-	-	11,0
Female (A)	9	165 + 615	455	1235	160	13,8
Female (A)	10	160 + 680	490	1330	153	13,0
Female (A)	11	160 + 560	450	1170	145	11,6
Male (S)	12	170 + 530	455	1155	175	12,3
Male (J)	8	675	405	1008	150	8,9

All males mean weight = 13,6 kg ± 2,37 (S.D.)
Adult females mean weight = 12,35 kg ± 1,11 (S.D.)
Adult males mean weight = 14,6 kg ± 1,58 (S.D.)

A = adult, S = sub-adult, J = juvenile

The 12 otters were caught a total of 17 times: one animal three times, three animals twice and the remaining eight only once. Table 14 gives the date and site of each capture or re-capture and the reactions of the otters to the drugs used for immobilization. Unfortunately the time to full recovery could not always be measured. This was usually the case with animals receiving a radio implant which necessitated a large booster. These animals recovered some time during the night after the operation, while not under observation.

Information on ectoparasites collected from 12 trapped otters is recorded in Appendix I.

TABLE 14

Reaction of otters to immobilization

No. of otter	Sex	Weight	Date of capture	Trap site number	Ketalar Dose (mg/kg)	Booster (mg/kg)	Aceto-promazine dose (mg/kg)	Booster (mg/kg)	Time after initial dose (mins)	Ataxia (mins)	Full recovery (hrs)
1	Male	15,5	25/5/81	2	12,9	3,2	1,0	0,5	30	3,5	5-
1	Male	15,5	27/7/82	1	8,8	-	0,8	-	-	3,5	<4
2 x	Male	17,8	26/5/81	2	11,2	11,2	0,9	-	240	4	>24
2	Male	17,7	22/6/82	4	7,1	5,5	0,7	1,1	135	4	>-
3 x	Male	13,0	3/9/81	5	10,0	-	1,0	-	-	8	-
4 x	Male	13,8	14/10/81	5	9,1	5,4	0,9	0,2	15	20	4
5 x	Male	1,35	3/12/81	1	11,1	3,7	1,0	-	10	15	-
5 +	Male	13,8	25/2/82	1	10,9	4,5	0,9	0,4	10	5	-
6 x	Female	11,0	4/2/82	10	11,4	-	0,9	-	-	4	-
7	Male	13,8	13/3/82	2	9,1	6,4	0,9	0,2	40	5	7-
7 x	Male	14,3	10/6/82	4	8,7	9,1	0,9	0,2	45	3	8
7	Male	13,2	21/7/82	1	9,5	-	0,8	-	-	11	<8
8	Male	8,9	4/5/82	5	14,0	5,6	1,2	0,1	16	20	-
9	Female	13,8	13/5/82	7	9,1	-	0,9	-	-	10	4-
10	Female	13,0	1/6/82	5	9,6	5,4	1,0	0,5	93	4	5-6
11	Female	11,6	18/7/82	4	10,8	5,4	0,7	0,2	220	12	10-
12	Male	12,3	16/8/82	8	13,2	6,0	1,1	0,3	35	20	8

Location of trap sites is shown in Figure 6 , with the exception of trap site 10 which lies west of the Groot River at Nature's Valley.

x Implantation of transmitter

\+ Removal of transmitter

POPULATION ESTIMATE

The first radio-isotope used in the population estimate was ^{51}Cr, with which only one otter was injected. Following its release at the Geelhoutbos River (Fig. 6) twenty-eight spraints were collected on the coast between Robsloep, approximately 2 km west of the Lottering River, and the western point of Bloubaai, a total distance of 7,5 km. However none of these spraints was detectably radio-active so no useful results were obtained.

Subsequently ^{65}Zn was used and spraints were collected over two widely separated sections of coast. The two release sites for the three otters injected were separated by 33 km, straight-line distance, of coast. Two otters were released at the Geelhoutbos at trap site 5, the other at a holt approximately 500 m west of Gammelbaai at trap site 7 (Figs 6 and 9). Spraints were monitored for radio-activity over a distance of 12,5 km either side of the Geelhoutbos and 14,3 km either side of Gammelbaai. The first otter released was number 8 at the Geelhoutbos on 4 May 1982, the second was number 9 near Gammelbaai on 13 May and the third was number 10 at the Geelhoutbos on 7 June.

Between 7 May and 8 June 843 spraints were tested for radio-activity in the field using the portable geiger counter. In this period only five spraints were recorded as being radio-active. Consequently all spraints subsequently located were collected for accurate counting in the laboratory. These later collections were made from 13 May to 28 August, when 446 spraints were collected from the western section and 517 from the eastern section.

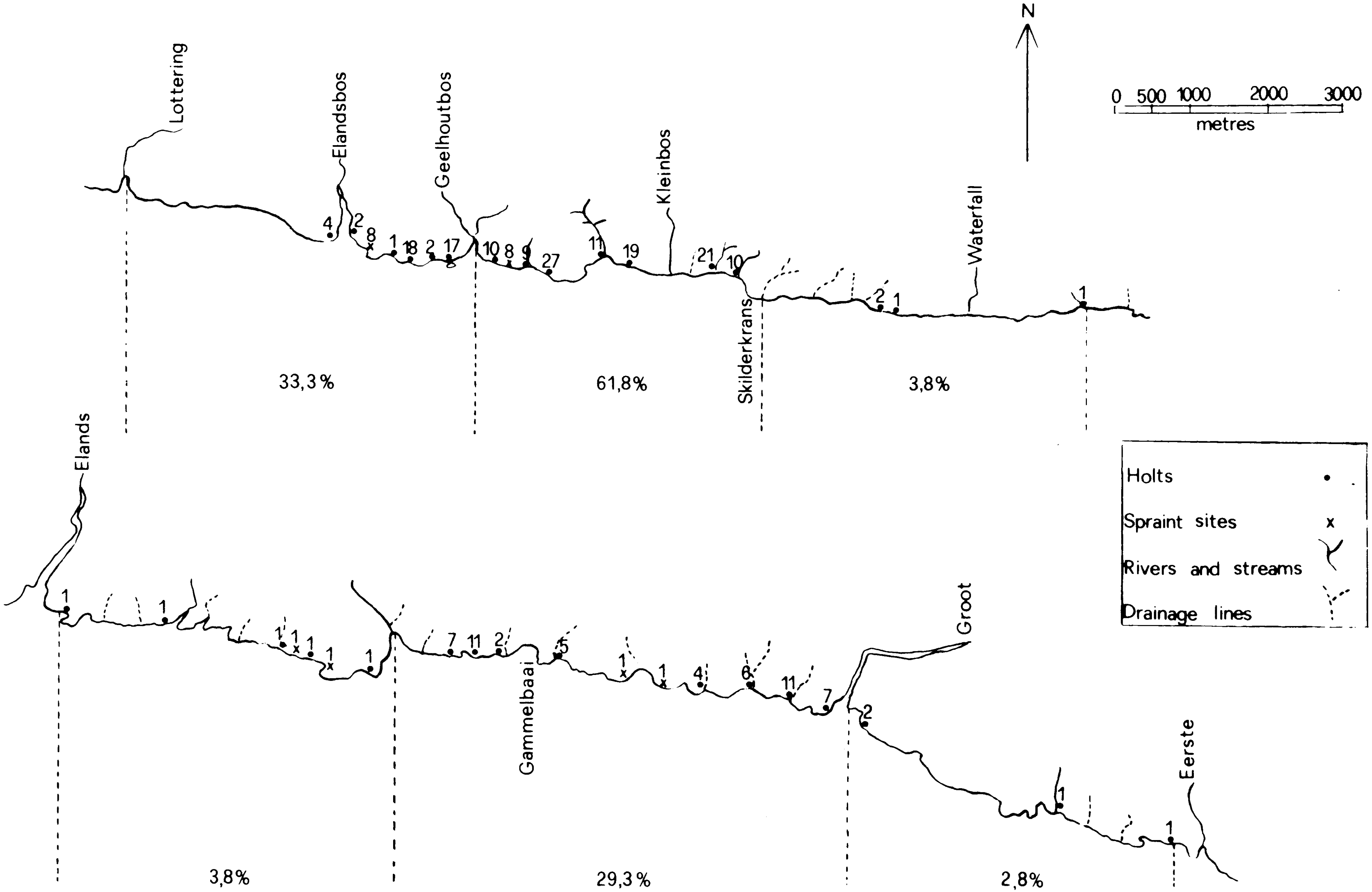


Fig. 9 Distribution of ^{65}Zn labelled spraints in two areas in the Tsitsikama Coastal National Park. June –

Percentages refer to proportion of sample that is

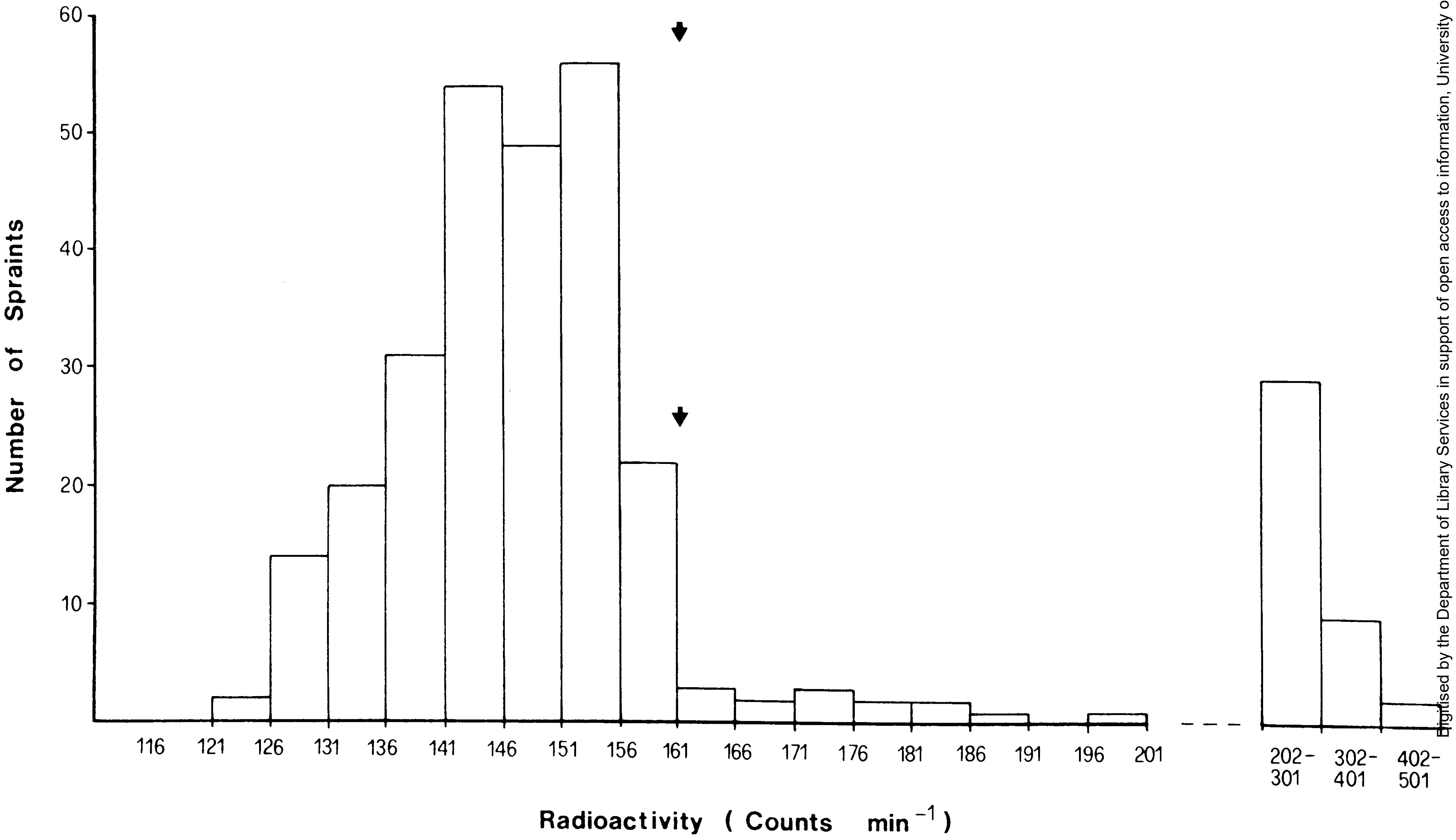
The final population estimate was based on all the 517 spraints from the eastern section, but only 418 of the spraints from the western section. Twenty-eight non-radioactive spraints were removed from the western sample because these were the only spraints found west of the mouth of the Elandsbos River. As none were radio-active it was not clear whether or not the range of either of the two otters released extended beyond the mouth of the Elandsbos. To ensure a valid estimate of population density it is necessary to sample only those spraints within the known range of the labelled animals i.e. between the easternmost and westernmost locations of radio-active spraints. Thus the western section effectively extended only 9,5 km from the west bank of the Elandsbos in the west to George se baai in the east.

In the case of the eastern section both the most easterly and the most westerly collection sites yielded radio-active spraints so the population estimate was valid for the full 14,3 km straight-line distance of the study area.

Figure 10 is an example of the frequency distribution of and counts of a sample of collected spraints. The normal distribution seen at the lower end of the scale represents the non-radioactive samples, displaying only small variations in background radiation. The statistical threshold calculated for this frequency distribution (see below) is marked on the figure. In all the samples the statistical limit coincided closely with the upper limit of the normal distribution, where this was distinguishable.

Table 15 presents the data used to calculate the statistical threshold between radio-active and non-radioactive spraints. The counts of radio-activity were made on two different machines, one of which gave a and non-radioactive spraints collected in the

Tsitsikama Coastal National Park, June - August 1982



consistently higher reading for background values, probably due to contamination of the machine. This necessitated two separate thresholds, one for each machine.

TABLE 15

Samples of least radio-active spraints used for calculation of the statistical threshold.

MACHINE 1									
Radio-activity counts per minute	121-125	126-130	131-135	136-140	141-145	146-150	151-155	156-160	161-165
Number of spraints	2	16	37	74	142	134	107	38	10

n	$\bar{x}$	σ	$\bar{x} + 1{,}96\sigma$
560	146,2	7,63	161,2

Test for normality $\chi^2 = 10{,}95$ with 7 df, $P > 0{,}10$ (Normal)

MACHINE 2							
Radio-activity counts per minute	106-110	111-115	116-120	121-125	126-130	131-135	136-140
Number of spraints	1	22	44	53	27	20	5

n	$\bar{x}$	σ	$\bar{x} + 1{,}96\sigma$
172	123,2	6,52	136,0

Test for normality $\chi^2 = 5{,}09$ with 4 df, $P > 0{,}20$ (Normal)

Once all the spraints had been monitored the radio-active counts at the lower end of the scale which appeared to conform to a normal distribution were separated from the remainder for statistical analysis. Table 15 shows the frequency distribution for the lowest nine classes of counts per minute (c.p.m.) from machine 1 and the lowest seven classes of machine 2. Both distributions were tested against normal distributions generated from the calculated mean and standard deviation shown in this table. The results showed that neither of these samples differed significantly from normality (machine 1, $\chi^2 = 10,95$ with 7 df, $P > 10$, i.e. not significant, and machine 2, $\chi^2 = 5,09$ with 4 df, $P > 7,20$, i.e. not significant).

The respective thresholds of the mean plus 1,96 standard deviations were then applied to the 678 spraints counted in machine 1 and the 285 spraints counted in machine 2. The threshold for machine 1 was 161,2 c.p.m. and for machine 2, 136,0 c.p.m. The statistical threshold for machine 1 is marked in Figure 10 which depicts a sample count from the eastern study area. It should be stressed that this is only a sub-sample of all the spraints monitored in machine 1.

Application of the statistical thresholds to the complete samples from machines 1 and 2 gave the results shown in Table 16.

TABLE 16

Numbers of labelled and non-labelled spraints collected in two study areas in the Tsitsikama National Park, June - August 1982

	Number of radio-active spraints	Number of non-radio-active spraints	Total
Elands-Eerste Rivier (East)	67	450	517
Lottering-Rietmondjie (West)	175	271	446
TOTAL	242	721	963

Using the formula (Kruuk, Gorman & Parish, 1980):

$$G = I \times \frac{N}{n+}$$

explained in the Methods, the population size for the two study areas can be calculated. Given a known length of coast this can be converted into population density for the study areas. The straight-line distance of coast for the two study areas and the calculation of population size are shown in Table 17 .

TABLE 17

Calculation of population density of <u>Aonyx capensis</u> in the Tsitsikama Coastal National Park, June - August 1982

	Number of otters labelled (I)	Number of radio-active spraints (n+)	Number of total spraints (N)	Population size (G)	Length of coast (SLD)	Population density $\frac{G}{SLD}$ = otters/km
Elands-Eerste Rivier	1	67	517	7,72	14,3 km	0,54
Elandsbos River - Rietmondjie	2	175	418	4,78	9,5 km	0,50

The estimate of population size for the western study area is based on a sample which does not include twenty-eight non-radioactive spraints collected west of the Lottering. The reasons for this modification to the technique are explained above.

The population density converts into an estimate of one otter every 1,85 km in the eastern study area (Elands to Eerste River) and one otter every 2 km in the western study area (Elandsbos River to

Rietmondjie). Taking the mean density as 0,52 otters per km for the whole of the Tsitsikama Coastal National Park which constitutes some 58,5 km, straight-line distance of coast, these figures give an estimated population size in the Park of 30-31 otters, or one otter every 1,9 km.

Radio-active spraint labelling also yielded data pertinent to the social organization of *Aonyx*.

In the eastern study area where only one labelled animal, an adult female was released, the distance between the most widely separated radio-active spraints provided a minimum estimate of her range size. As radio-active spraints were found at the most easterly and the most westerly collecting points this minimum estimate corresponded to the full length of the study area, 14,3 km. Within this stretch of coast radio-active spraints were found at thirteen known holts (Fig. 9) and three spraint sites. Individual radio-active spraints were found at two other locations.

Of the 67 radio-active spraints located, 55 were found between Jaftaskraal and the Groot River at Oubosstrand. Thus 82% of the radio-active spraints were confined to a 5,7 km central section of the known range of the female.

The distribution of radio-active spraints in the western study area, between the Elandsbos River and Rietmondjie provide some information on the ranging behaviour of females with respect to the loose boundaries that radio-tracking results indicate for males (page 177).

The situation was confounded by the fact that two labelled otters were released at the Geelhoutbos, one an adult female and the other an immature male. However considering the size of the male (8,9 kg), his sexual immaturity and the fact that an adult otter threatened me from the nearby holt it seems likely that the animal was still accompanied by its dam. Assuming that this was indeed the case throughout the period in which spraints were collected, the movements and holt utilisation of the immature male would accurately reflect those of its dam.

Even if this were not the case, so long as the marked female was also depositing radio-active spraints, the interpretation of a restricted distribution of spraints would still apply to female behaviour.

The validity of the population estimate for both the western and eastern sections depended on the assumption that none of the labelled otters died or moved out of these areas during the collection of spraints.

The restriction of the distribution of radio-active spraints was very strictly defined in this western study. West of Skilderkrans a total of 337 spraints were sampled, of which 171 (50,7%) were radio-active. East of Skilderkrans a total of 109 spraints were sampled of which only 4 (3,7%) were radio-active. As 31 radio-active spraints were found in 0,5 km immediately west of Skilderkrans (Fig. 9) and only 4 radio-active spraints in 4,5 km immediately east of Skilderkrans, it would appear that neither labelled otter frequently visited the coast west of this point.

Interpretation of holt utilisation for the western study area is not as straightforward or rewarding as for the eastern study area, due to the presence of two labelled otters in the former area. All that can be said is that between them, these two otters utilised a total of ten holts between the Elandsbos and Skilderkrans regularly and three holts east of Skilderkrans on only one or possibly two occasions. Three spraint sites west of Skilderkrans were also regularly used.

Though no radio-active spraints were found to the west of the Elandsbos only 28 spraints were sampled west of this point and it would not be safe to assume that the Elandsbos represents the western extent of the labelled animals' range.

RADIO-TRACKING

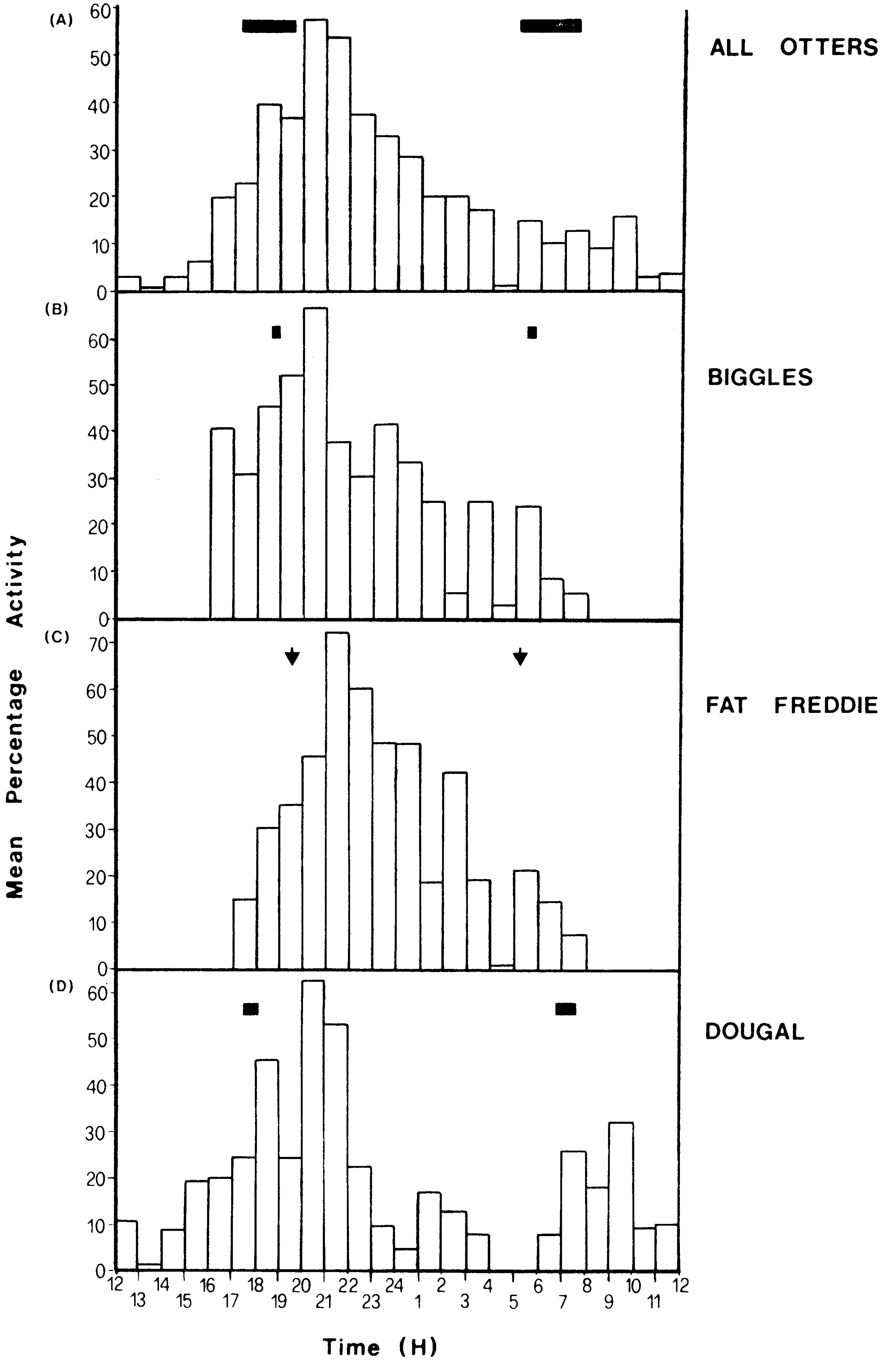
Information obtained in the course of this radio-tracking study relates to the otters' use of time and space, foraging and predatory behaviour and social organization. The results are presented in order of increasing detail with data on activity patterns and range size presented first, then data on range and holt utilisation, on analysis of foraging patterns with respect to time and environmental conditions next, followed by detailed observations on the predatory behaviour of *Aonyx*. Finally data on social behaviour gained both from radio-tracking, from opportunistic observations by the author and staff and visitors in the Park are presented.

ACTIVITY PATTERN

The activity patterns of three otters, Biggles, Fat Freddy and Dougal, are shown combined (Fig. 11 a) and then separately for each otter (Fig. 11(b), (c) & (d)). The three activity patterns for individual otters contribute equally to the combined activity pattern in Figure 11 (a), though the sample sizes on which the individual activity patterns were based vary considerably in size.

The results are based entirely on radio-tracking. For each one hour period the total time in contact with the animal is recorded. The proportion of this time during which the animal was active is expressed as a percentage. Thus for example Dougal was tracked for a total time of 630 minutes between 01h00 and 02h00. For 522 minutes of this sample Dougal remained inactive while for the remaining 108 minutes (17,1%) he was active.

Arrows and blocks indicate the time of sunset and sunrise during the tracking period



g. 11 Activity patterns of three radio-tracked adult male *Aonyx capensis* in the Tsitsikama Coastal National Park, October 1981 - August 1982

In Figure 11(d) the percentage activity values for each hourly period for the three otters are summed and then divided by three with the exception of the two periods 08h00 - 09h00 and 09h00 - 10h00. For these periods no data on Biggles' activity pattern are available. The final combined estimate of activity between 08h00 and 10h00 was based on the summed percentage activities of Dougal and Fat Freddy divided by two. In Figure 11(a) Biggles is recorded as being 0% active in this period, due to the complete absence of a sample. However, this may not be an accurate reflection of the true situation.

Daily patterns of foraging activity are illustrated in Figure 12 The data relate to three radio-tracked males: one tracked in spring (Biggles), one in summer (Fat Freddy) and one in winter (Dougal). The movements of the otters during these radio-tracks are illustrated in Figs 15 and 16 later in this section.

Using the accumulated data presented in the histograms the mean level of activity, expressed as a percentage of the total time during which the animal was under observation, was calculated for four periods during the day. These periods were day, night, the hour in which sunrise occurred and the hour in which sunset occurred. The sunrise and sunset periods were examined to check for crepuscular peaks of activity and to compare activity levels at dusk and dawn.

The mean percentage activity for these four periods, the daily mean percentage activity, the nocturnal : diurnal ratio of mean percentage activity and the mean sea temperature during the tracking periods are recorded in Table 18.

four continuous tracks in the Tsitsikama Coastal
National Park, October 1981 - July 1982

blank = resting. Arrows indicate sunrise and sunset.

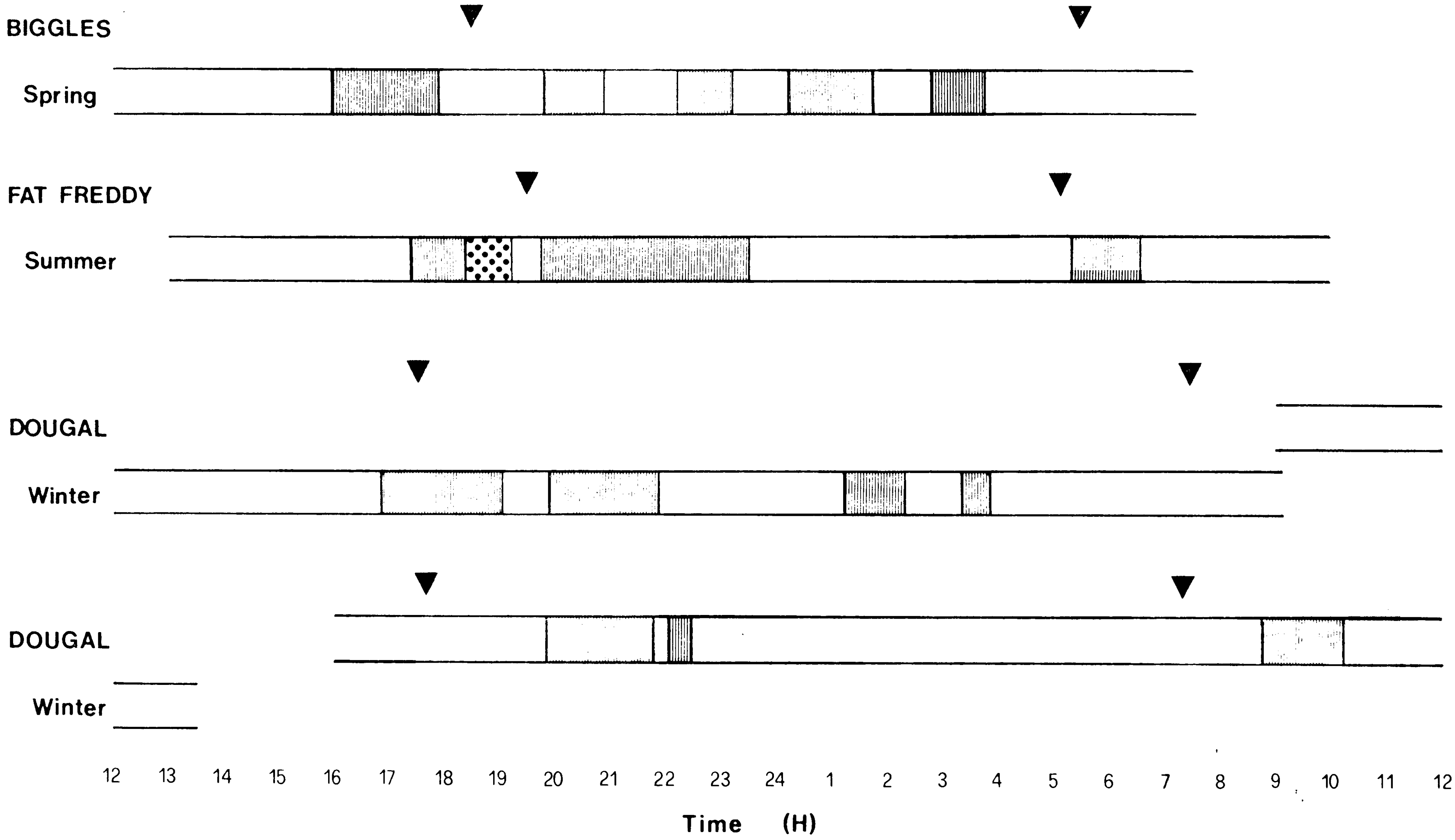


TABLE 18

Mean percentage activity of three adult male <u>Aonyx</u> during different periods of the day on the Tsitsikama coast, October 1981 - August 1982

Otter	Period of tracking	°C Mean sea temp. during tracking	Mean %age activity daytime	Mean %age activity nighttime	Mean %age activity sunrise hour	Mean %age activity sunset hour	Mean %age activity 24 hours	Ratio %age activity nocturnal: diurnal
Biggles	19/10/81- 2/11/81	17,51	13,1	33,9	24,0	45,4	25,0	2,59:1
Fat Freddy	9/12/81- 22/12/81	18,49	10,4	40,9	21,7	35,6	25,0	3,93:1
Dougal	16/6/82- 28/7/82	15,44	14,7	20,7	26,0	24,4	18,2	1,41:1

The mean percentage activities recorded above were calculated from the total sample for the specified period. These samples were not standardised with respect to hourly intervals as Biggles and Fat Freddy were subject to reduced radio-tracking in coverage in the middle of the day. As their activity appeared to be much reduced at this time of day, the results given above probably overestimate their diurnal activity to some extent. Therefore the contrast in nocturnal:diurnal activity ratios between Dougal on the one hand and Biggles and Fat Freddy on the other is, if anything, greater than that shown above.

All three otters display significant variation in mean percentage activity during the four periods of the day. Biggles favoured night and the sunset hour for foraging but tended to avoid foraging during the day (χ^2 = 294,5, 3 df, P < 0,001). Fat Freddy behaved in a similar fashion (χ^2 = 811,8, 3 df, P < 0,001) though his preference for nocturnal foraging was even more marked than was Biggles'. Dougal showed a preference for foraging nocturnally and at sunset and sunrise (χ^2 = 177,2, 3 df, $P < 0{,}001$). However activity levels at night were considerably lower than in the other animals and though activity levels were still at their lowest during the day, this tendency was not as pronounced as in the other two animals. The variation between the three otters in both diurnal activity levels (χ^2 = 40,41, 2 df, $P < 0{,}001$) and nocturnal activity levels (χ^2 = 501,1, 2 df, $P < 0{,}001$) is statistically significant.

RANGE SIZE

The estimate of range size of an animal increases progressively during radio-tracking as the number of radio fixes on which the estimate is based increases. This progressive increase is illustrated in Fig. 13 in which known limits of the range are plotted against the total number of radio fixes for four of the otters. This has considerable implications for the interpretation of results obtained in this study and these are discussed later.

The proportion of radio-tracking days on which each animal was located is shown in Table 19.

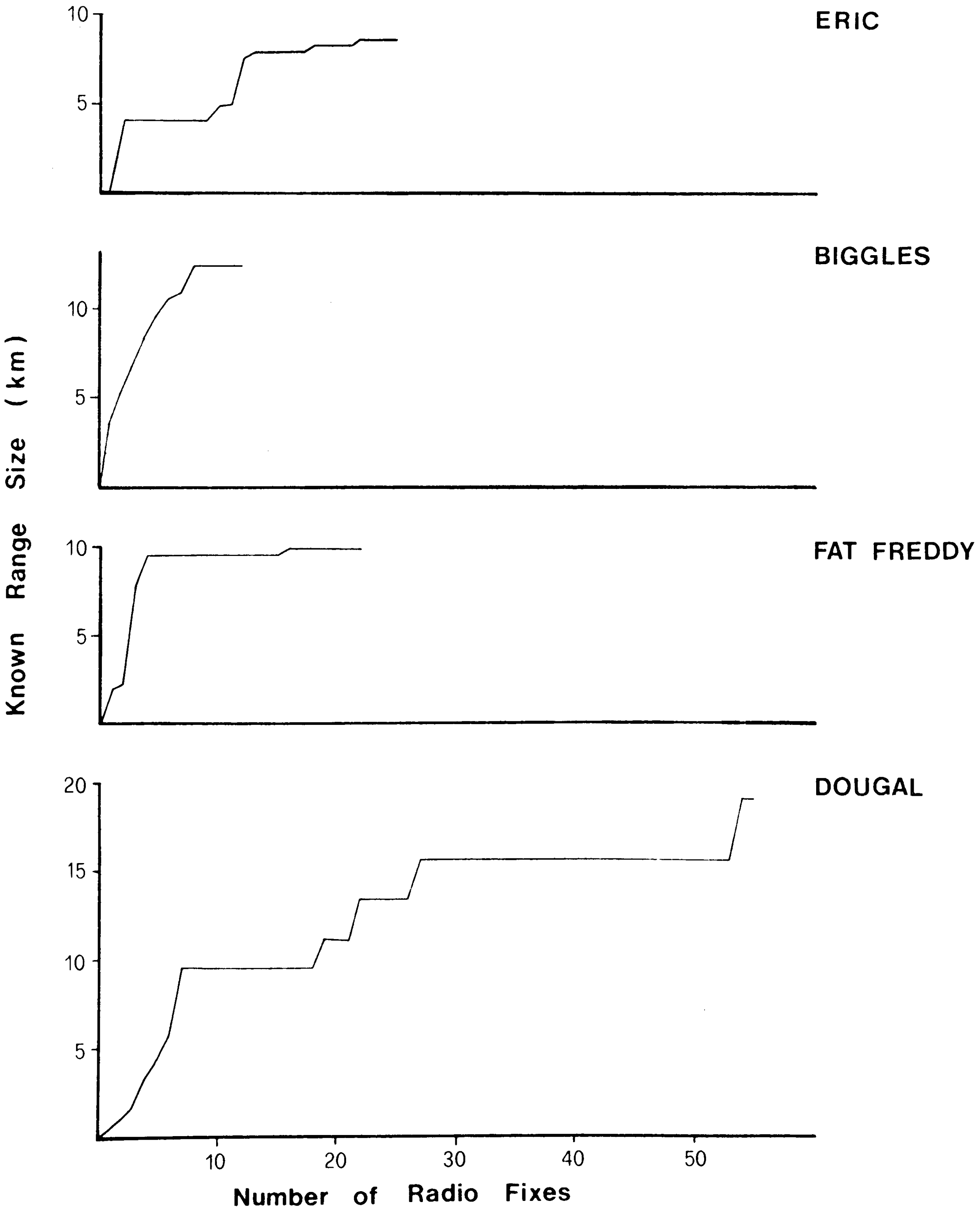
TABLE 19

Proportion of radio-tracking days on which instrumented *Aonyx capensis* were located in the Tsitsikama Coastal National Park, June 1981 - August 1982.

Otter	ERIC	NAFFER	BIGGLES	FAT FREDDY	DOUGAL
Days tracked	24	6	13	18	47
Days located	16	5	12	16	44
Ratio days located: days tracked	0,67	0,83	0,92	0,89	0,94

These results provide an indication of the improvement in radio-tracking success. They may also be used to assess the proportion of time spent within the known limits of a range, if the actual limits are believed to exceed the known limits (see Discussion).

Fig. 13 Progressive increase in known range of radio-tracked *Aonyx capensis* as the number of radio fixes accumulate



The known limits of ranges of five males radio-tracked during the study, plus that of a sixth that was sighted in the company of one of the radio-tagged animals, are shown in Fig. 14 . The trap site or sites of each animal are indicated by a figure corresponding to that allocated to the animal in Table 11 (see trapping results).

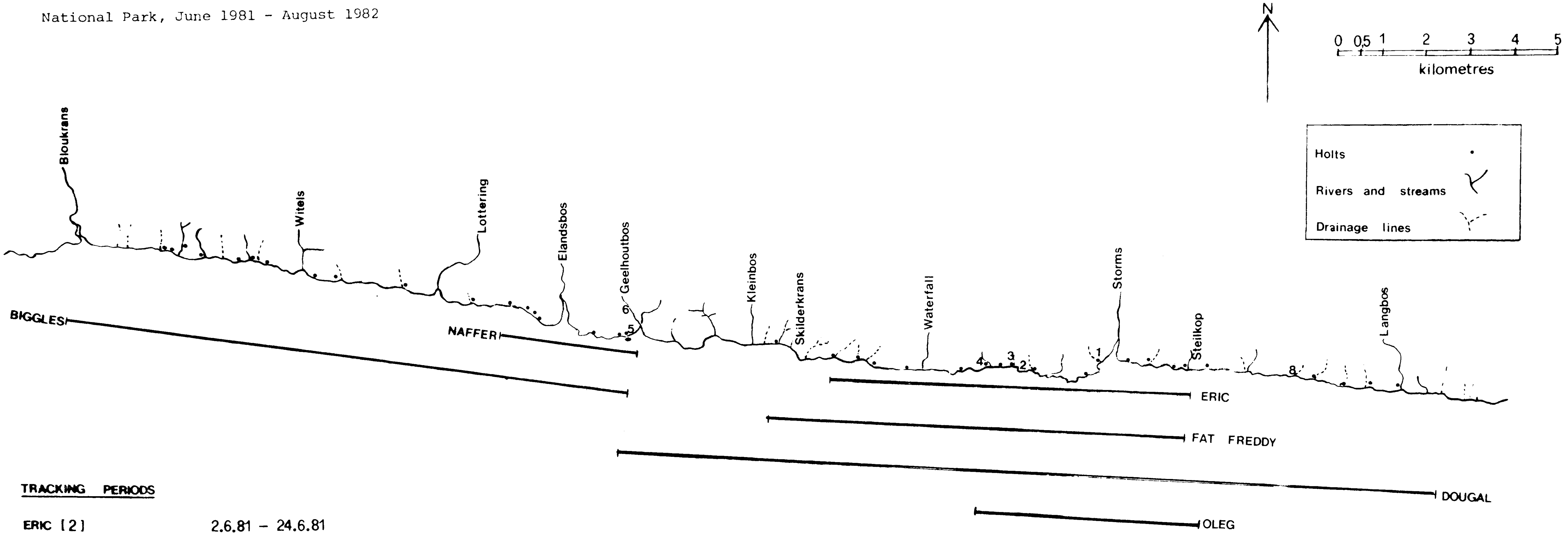
MOVEMENT PATTERNS

A complete graphic record of all the movements of each otter tracked is not presented. The linear range dictates considerable use of space for such representations which can only be justified for those tracks which serve to illustrate a particular behaviour pattern.

The tracks illustrated in Figs 15 - 17 are for four different otters and are based either on a single daily fix over periods of six to eleven days (Figs 15a - 16 a-d) or on a single continuous track of one otter through a complete night and part of the day before and after (termed "night tracks", Figs 15 b & c and 17 a-d). These tracks have been selected to illustrate particular points raised in the discussion.

Detailed analysis of the foraging patterns displayed by *Aonyx* is presented in a later section. Only the frequency of course reversal in foraging movements is analysed here. Course reversal occurs when, in the course of a single foray, an animal covers any section of coast more than once. Five statistical tests were used to test for individual variation in the frequency of course reversals between diurnal and nocturnal foraging of individual otters (Table 20).

Fig. 14 Known range sizes of six adult male <u>Aonyx capensis</u> determined by radio-tracking in the Tsitsikama Coastal National Park, June 1981 - August 1982



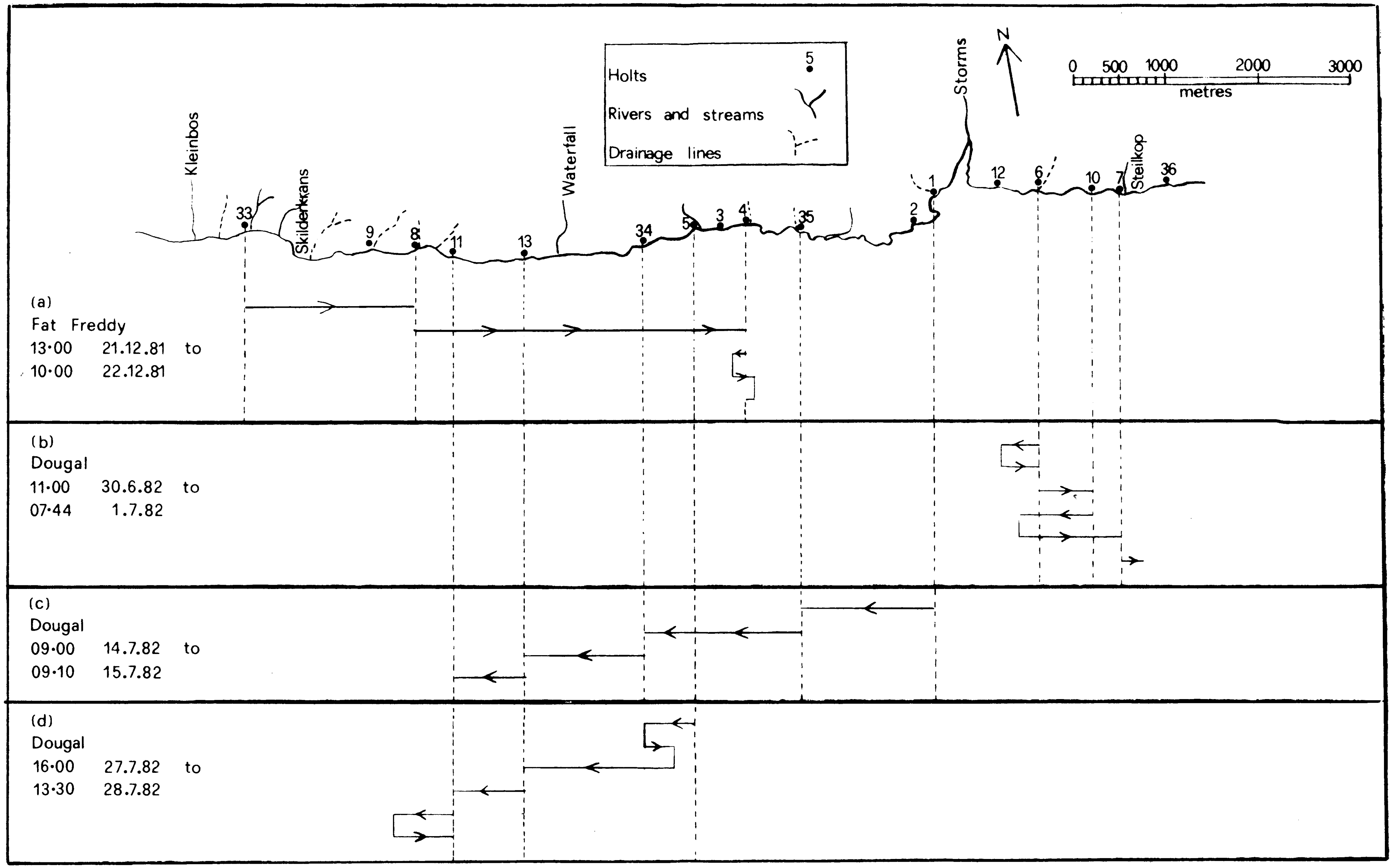
TRACKING PERIODS

ERIC [2]	2.6.81 - 24.6.81
NAFFER [3]	8.9.81 - 13.9.81
BIGGLES [4]	19.10.81 - 2.11.81
FAT FREDDY [5]	9.12.81 - 13.1.82
DOUGAL [7]	16.6.82 - 26.8.82
OLEG [1]	12.8.82 - 13.8.82 (accompanying Dougal)

LINEAR EXTENT OF KNOWN RANGES

ERIC	8,6 km
NAFFER	3,3 km
BIGGLES	13,3 km
FAT FREDDY	10,0 km
DOUGAL	19,5 km
OLEG	5,4 km

Fig. 16 Four continuous tracks of two adult male <u>Aonyx capensis</u> in the Tsitsikama Coastal National Park between December 1981 and July 1982



'ig. 17 Daily fixes for three adult male *Aonyx capensis* in the Tsitsikama Coastal National Park between June 1981 and July 1982

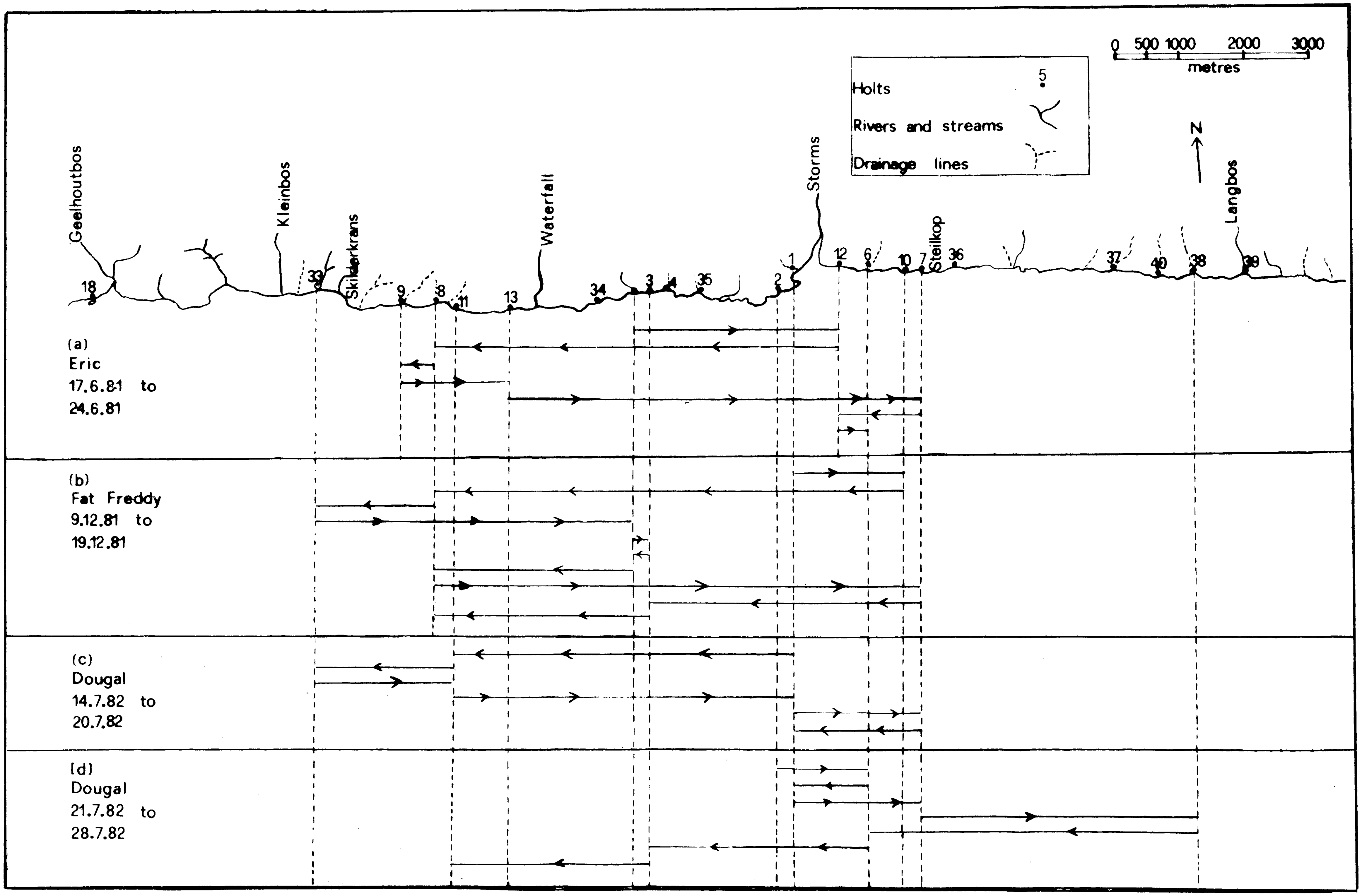


TABLE 20

Statistical analysis of the frequency of course reversal in three adult male Aonyx capensis radio-tracked in the Tsitsikama Coastal National Park, October 1981 - August 1982.

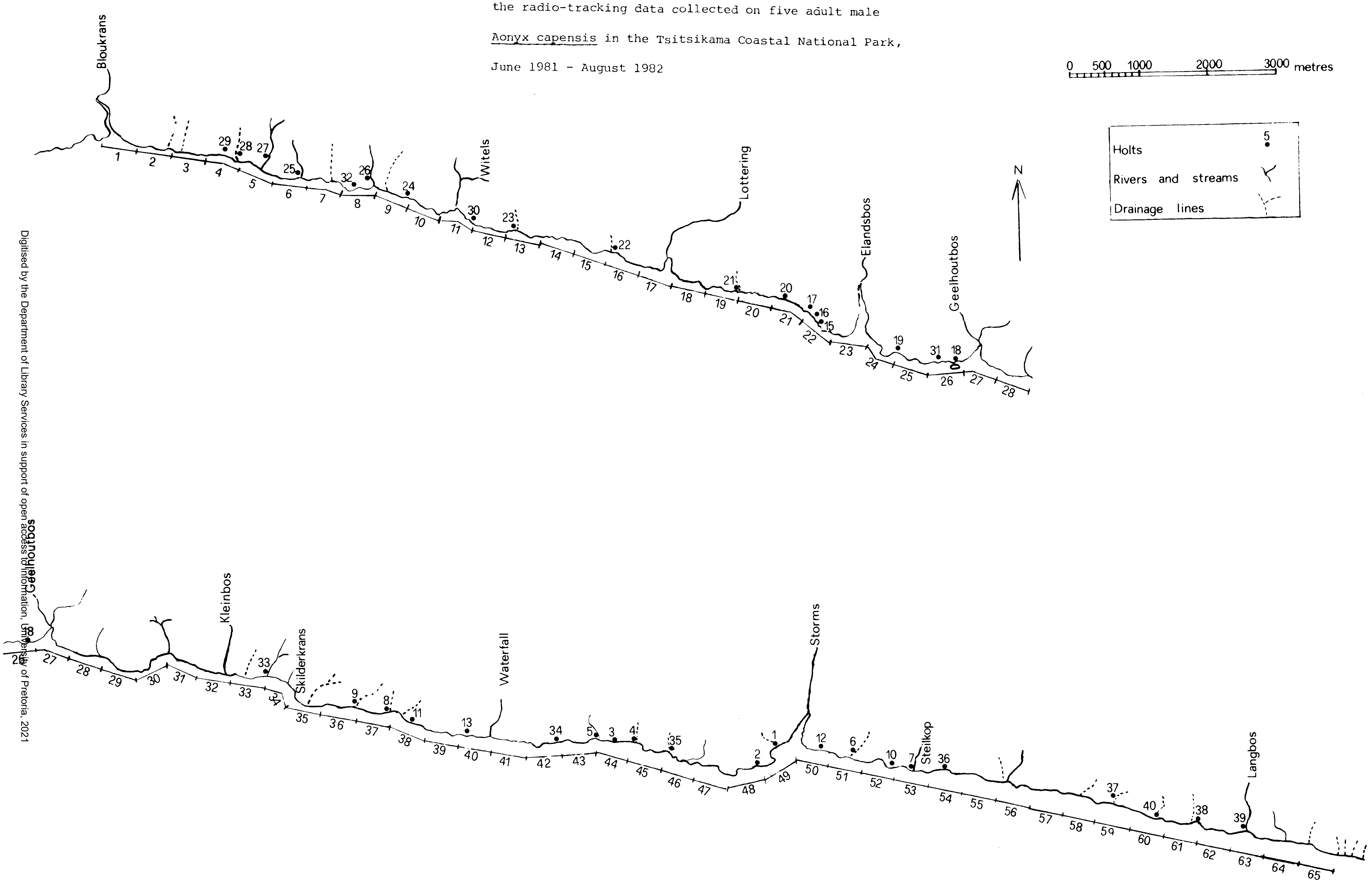
VARIABLES TESTED	TEST	RESULTS	INTERPRETATION
Biggles: Frequency of course reversal - day vs. night	Fisher Exact Probability Test	P=0,50	N.S.
Fat Freddy: Frequency of course reversal - day vs. night	"	P=0,027	Significantly fewer course reversals at night
Dougal: Frequency of course reversal - day vs. night	χ^2 Test	χ^2=0,37, 1 df P>0,50	N.S.
All otters: Frequency of course reversal - day vs. night	"	χ^2=1,94, 1 df P>0,10	N.S.
Frequency of course reversal: Biggles vs. Fat Freddy vs. Dougal	"	χ^2=1,52, 2 df P>0,10	N.S.

The results of this analysis indicate that only one of the three otters, Fat Freddy, displayed a significant variation in the frequency of course reversal between night and day. Furthermore there was no significant variation in the frequency of course reversals between individuals.

RANGE UTILISATION

For the analysis of range utilisation and foraging patterns with respect to time and environmental conditions, the ranges of the tracked animals were divided into sections of 500 m, straight-line distance (Fig. 18). A total of 65 such sections covered the known ranges of the

Fig. 18 500 m sections of coast and holt numbers referred to in the radio-tracking data collected on five adult male *Aonyx capensis* in the Tsitsikama Coastal National Park, June 1981 - August 1982



five adult males that were tracked (Fig. 14).

Two methods were used to score range utilisation; the total time spent foraging in a section and the number of times an animal was initially located in a section or moved into that section during radio-tracking. These alternative methods provided a cross-check. If there is considerable disagreement in the results obtained using the different methods then one or both methods is invalid.

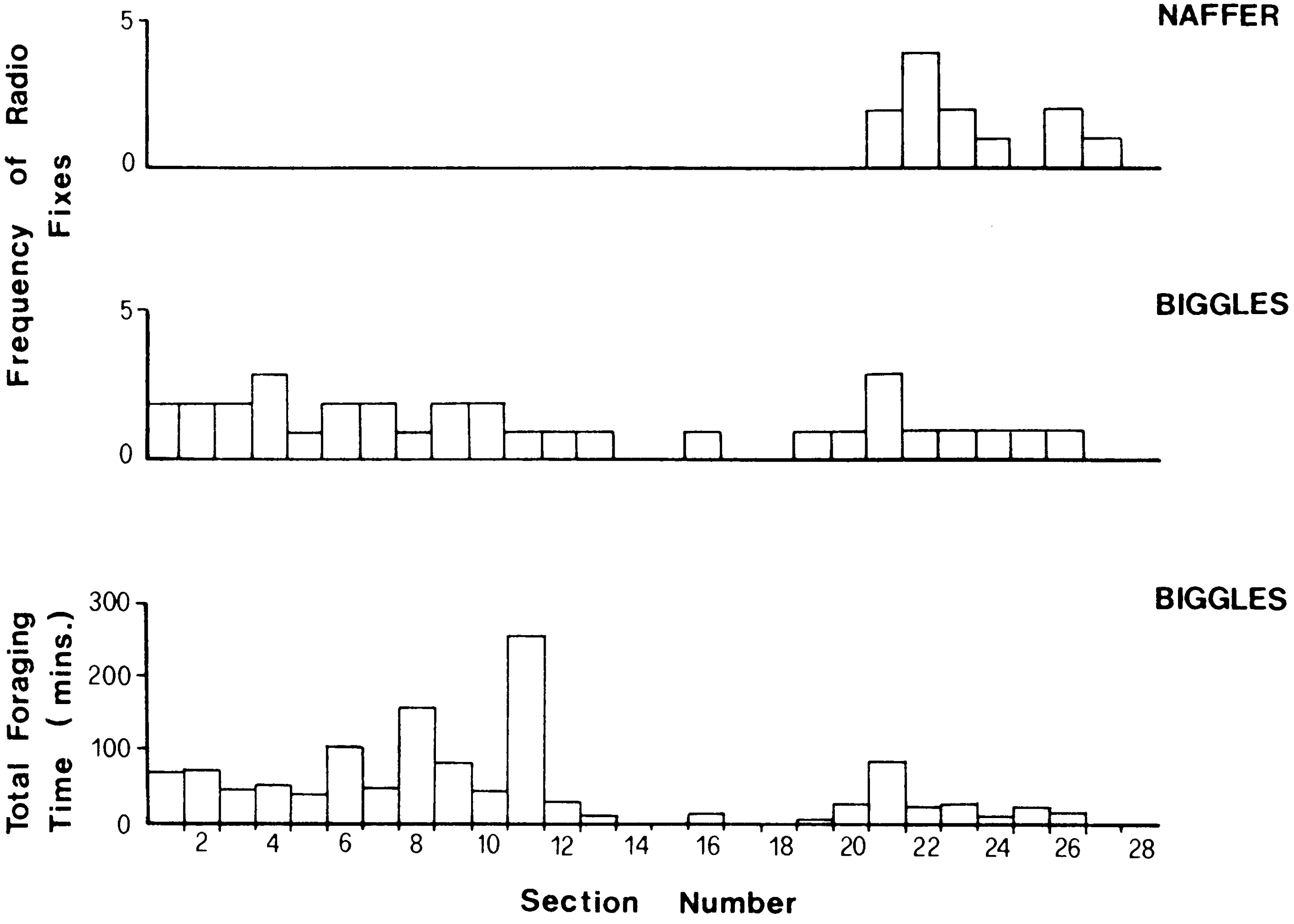
If there is general agreement between the results obtained from the two methods, the validity of the technique is to a large extent confirmed. However, there remains the possibility of a common error affecting both measures.

Correlation between the two methods of scoring range utilisation was measured for those animals on which enough data had been collected, namely Fat Freddy and Dougal. Sections which received only two visits or less from the otters were excluded from the test. Spearman's rank correlation coefficient was used and in both cases there was a significant correlation between the two methods of scoring range utilisation (for Fat Freddy, $r_s = 0{,}646$, $N=12$, $P<0{,}05$, significant; and for Dougal $r_s = 0{,}884$, $N=18$, $P<0{,}01$, significant).

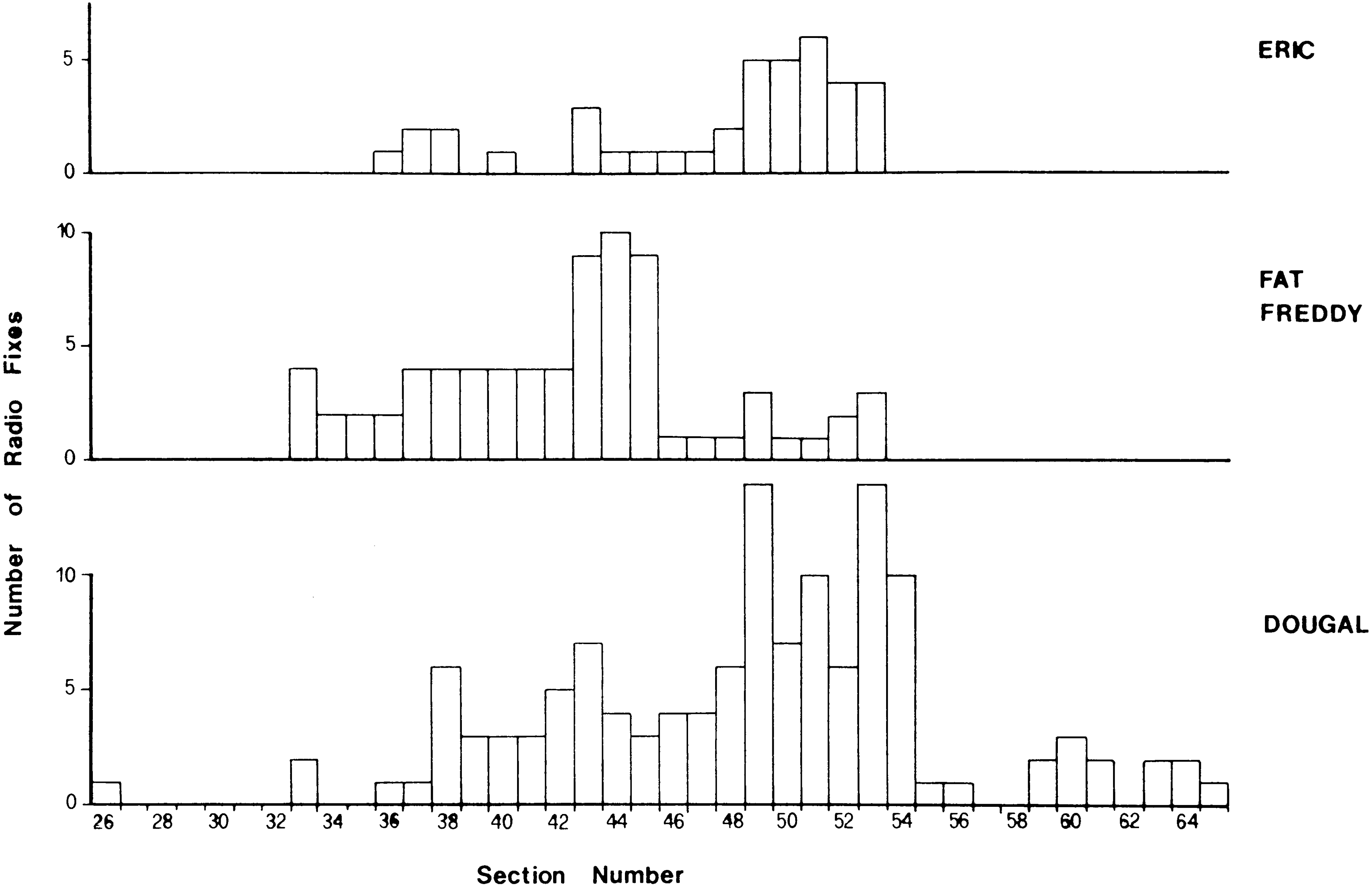
Examination of the histograms in Figs 19,20 & 21 reveals considerable variation in the levels of utilisation of different sections of an animal's range. The sample sizes collected during the radio-tracking of Naffer and Biggles were too small for statistical analysis. Sample sizes for Eric, Fat Freddy and Dougal were sufficient for analysis, the results are presented in Table 21.

adult male *Aonyx capensis* in the Tsitsikamma Coastal

National Park, September - November 1981



adult male *Aonyx capensis* in the Tsitsikama Coastal National Park, June 1981 - August 1982



National Park, June 1981 - August 1982

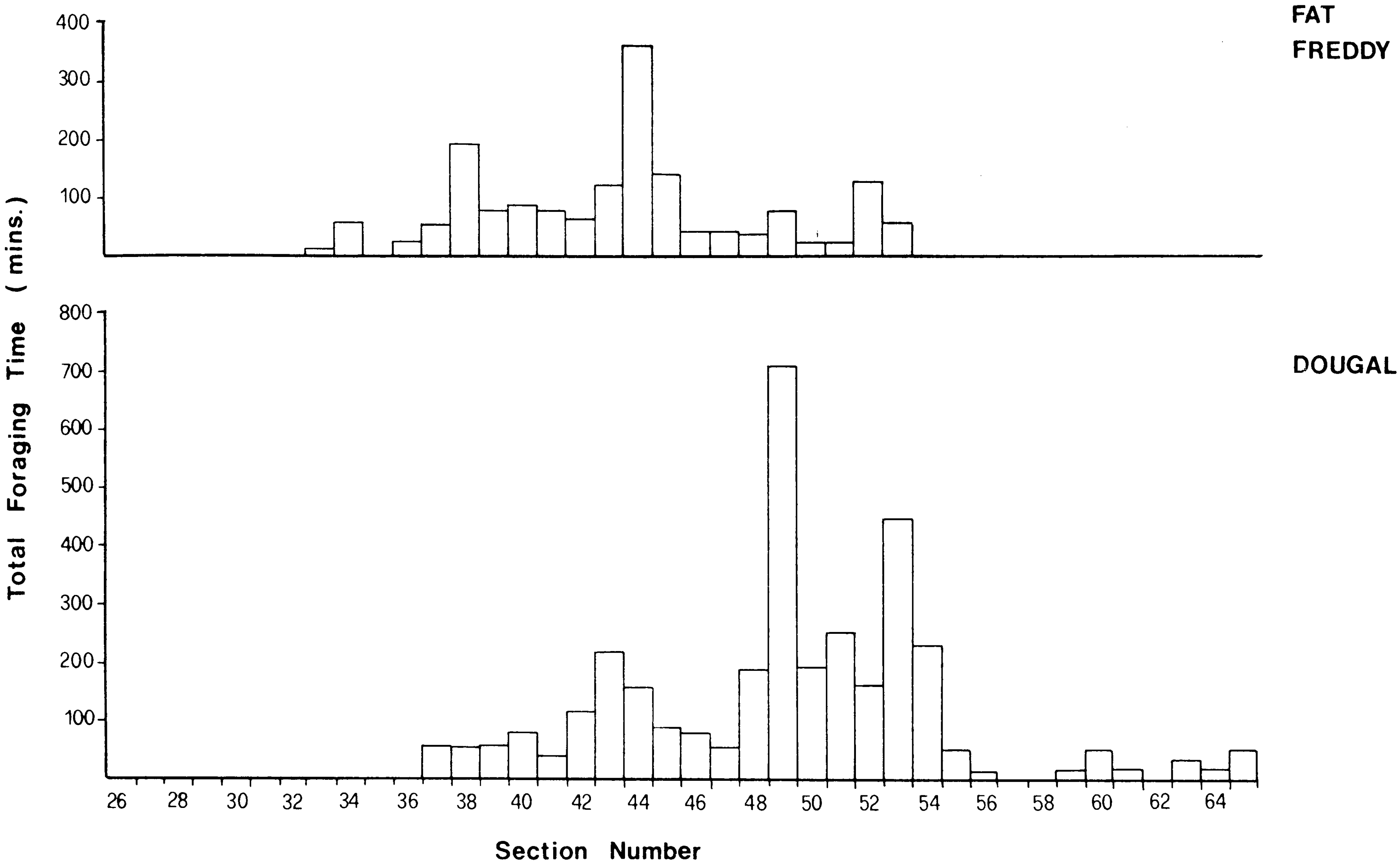


TABLE 21

Statistical analysis of variation in range utilisation in three male *Aonyx capensis* radio-tracked in the Tsitsikama Coastal National Park, December 1981 - August 1982

Otter	Measure of utilisation	Sections of coast compared	Test	Result	Interpretation
Eric	Frequency of fixes	49-53 vs. 36-48	χ^2	$\chi^2=5,73$, 1df $P<0,05$	Significantly higher utilisation of 49-53
Fat Freddy	Frequency of fixes	43-45 vs. 33-42 and 46-53	χ^2	$\chi^2=4,02$, 1df $P<0,05$	Significantly higher utilisation of 43-45
Dougal	Frequency of fixes	49-54 vs. 26-48 and 55-65	χ^2	$\chi^2=13,68$, 1 df, $P>0,001$	Significantly higher utilisation of 49-54
Dougal	Frequency of fixes	38-54 vs. 26-37 and 55-65	χ^2	$\chi^2=29,5$, 1 df, $P<0,001$	Significantly higher utilisation of 38-54
Dougal	Frequency of fixes	49-54 vs. 38-48	χ^2	$\chi^2=2,47$, 1 df, $P>0,10$	No significant difference in utilisation

The separation in the areas of peak range utilisation of Fat Freddy and Dougal is confirmed by the absence of a significant positive correlation in their frequency of occurrence in sections 38-53 (Spearman's rank correlation coefficient: $N=16$, $r_s = -0,362$, $P>0,05$).

Only one measure of utilisation was used throughout the statistical analysis to facilitate comparison of the results. Frequency of fixes per section was selected for the analysis. Total foraging time per section was more susceptible to bias due to variation in the distance of the section from the centrally placed starting point for radio-tracking searches (see Discussion).

HOLT UTILISATION

Three measures of holt utilisation were used, two based on the number of times the holt was used by the animal and the other on the total time spent in the holt. The simplest measure recorded the number of times each holt was used by the otter. To provide a better indication of any preference the otter might show for using a particular holt, the measure of occurrence in a holt was expressed as a ratio hereafter known as the utilisation ratio. This was calculated as the number of times a holt was used divided by the total number of times the holt was passed. Thus, for example, if a holt was passed five times and used only three times, the utilisation ratio is:

$$\frac{3}{5} = 0{,}60.$$

In the results utilisation ratios are only calculated for those holts which were passed three or more times by the otter. Total time spent in the holt is shown for all holts.

Correlation between the different measures of holt utilisation was checked using the data collected for Fat Freddy and Dougal. Sample sizes for Biggles were not large enough to give meaningful results.

The correlation between the total number of visits to a holt and the total time spent in the holt was significant for both animals (Fat Freddy, Spearman's rank correlation coefficient: $N=12$, $r_s = +0{,}646$, $P<0{,}05$; and Dougal $N=18$, $r_s = +0{,}884$, $P<0{,}01$). The correlation between holt utilisation ratio and total time spent in the holt is significant for Dougal (Spearman's, $N=12$, $r_s = 0{,}822$, $P<0{,}1$) but not for Fat Freddy ($N=11$, $r_s = 0{,}374$, $P>0{,}5$). This suggests that the holt utilisation ratio is not a reliable measure when calculation of the ratio is based on small

TABLE 22

Holt utilisation of five radio-tracked male _Aonyx capensis_ in the Tsitsikama Coastal National Park, June 1981 - August 1982

Eric	Holt number	9	8	11	13	5	1	12	6	7										
	Number of visits	1	1	2	1	2	1	2	2	3										
Naffer	Holt number	17	16	15	19	18														
	Number of visits	1	2	3	1	1														
Biggles	Holt number	29	28	27	25	32	26	24	30	23	22	21	20	19	31	18				
	Number of visits	2	1	1	1	1	2	5	3	1	1	1	5	1	1	1				
	Holt utilisation ratio	-	-	-	0,33	0,33	-	1,0	0,75	-	-	-	1,0	-	-	-				
	Time spent in holt (mins)	450	225	65	260	80	175	949	385	90	20	155	450	52	20	20				
Fat Freddy	Holt number	33	8	11	13	5	3	4	1	10	7									
	Number of visits	3	4	2	1	5	4	9	3	3	3									
	Holt utilisation ratio	1,0	1,0	0,5	0,25	0,83	0,57	1,0	1,0	0,75	1,0									
	Time spent in holt (mins)	295	150	288	30	993	1267	966	190	556	562									
Dougal	Holt number	18	33	9	11	13	34	5	4	35	2	1	6	10	7	36	37	40	38	39
	Number of visits	1	2	1	5	2	3	5	2	3	1	19	8	1	13	5	2	1	2	2
	Holt utilisation ratio	-	-	-	1,0	0,67	0,60	0,71	0,50	0,75	0,14	1,0	0,73	0,14	1,0	0,63	-	-	-	0,67
	Time spent in holt (mins)	125	595	185	1598	78	886	497	47	177	10	5237	1949	50	3484	501	356	35	162	755

samples.

The holt utilisation for all five otters, namely Eric, Naffer, Biggles, Fat Freddy and Dougal is presented in Table 22 . Only the holts visited and the number of visits are presented for Eric and Naffer, as the radio-tracking data for Eric was too fragmentary and Naffer was only tracked for five days. The total number of holts used by all five animals, the known extent of their ranges, and holt density based on these figures are presented in Table 23 .

TABLE 23

Extent of known ranges and density of holts used within the known range of five male <u>Aonyx capensis</u> in the Tsitsikama Coastal National Park, June 1981 - August 1982

	Eric	Naffer	Biggles	Fat Freddy	Dougal
Extent of known range	9	5	15	10	19
Holts used in known range	8,5	3,2	13,0	9,8	19,2
Holt density (holts/km)	1,1	1,6	1,2	1,0	1,0

The location of all the numbered holts is shown in Fig. 18 The known extent of ranges is illustrated in Fig. 6.

The holt utilisation data were compared with data on range utilisation and foraging behaviour recorded during radio-tracking and spraint distribution recorded during the coastal survey. The results on spraint distribution collected during the coastal survey offer a method of assessing the overall utilisation level of a particular holt.

Comparison of range utilisation and holt utilisation was made by testing for correlation between the number of visits to a particular holt (see Table 22) and the total foraging time recorded in the immediately adjacent sections of coast. Where a holt occurred in the middle of a section, the total foraging time for that section alone was compared with the number of visits to the holt. Where a holt occurred close to the borderline between two sections (within 100 m of this line) the total foraging time for the two sections was summed and divided by two and this mean was compared with the number of visits to the holt. Holts which were visited less than three times in the course of radio-tracking were not included in the comparison.

There was a significant positive correlation between holt utilisation and total foraging time spent in the adjacent sections of coast for both Fat Freddy (Kendall's rank correlation coefficient: $N=8$, $S=17$, $T=+0,70$, $P<0,01$) and Dougal (Kendall's rank correlation coefficient: $N=8$, $S=20$, $T=+0,77$, $P<0,005$).

The duration of the rest periods in holts varied widely, the shortest recorded being 15 min and the longest in excess of 24 hours. The mean duration of 59 completed rest periods recorded for Biggles, Fat Freddy and Dougal was 171,4 minutes. However the longest rest periods are under-represented as monitoring was often terminated during such rest periods. Duration of the rest was therefore unknown and could not be included in the sample.

Sufficient rest periods (N=28) were timed for Dougal to allow statistical analysis of the variation in rest period lengths at different holts. The result indicated that the six holts tested (holts 1, 6, 7, 13, 34 and 36) showed no consistent variation in the duration of rest periods (Kruskal Wallis Test: N=28, H=3,78, 5 df, P>0,50).

The patterns of holt utilisation of individual otters may be affected by the behaviour of the other otters sharing their home range (clan members - see Social organisation). There are sufficient data on Fat Freddy and Dougal to test for a correlation in the frequency of utilisation of ten holts lying between the Kleinbos River and Arrie se baai. Only the holts used at least once by Fat Freddy were included as this animal was only tracked for two weeks. Failure to use a holt in this short period was therefore not necessarily representative of the normal level of utilisation of that holt.

There was no significant correlation between the levels of utilisation of the ten holts by Dougal and Fat Freddy (Spearman's rank correlation coefficient: N=10, r_s = -0,268, P>0,05). A longer period of tracking is required to confirm this.

The holt utilisation data recorded for Fat Freddy and Dougal were combined for comparison with the holt utilisation data collected during the coastal survey. The number of recorded visits of the two animals to each holt were summed and divided by two to provide an estimate of mean utilisation rate. This was compared with the total number of spraints found at each holt in the course of the four-month monitoring period. Kendall's rank correlation coefficient was calculated for the two measures of holt utilisation recorded for eight holts lying between George se baai and Steilkop (holts 34, 5, 4, 1, 12, 6, 10 and 7, Fig. 18 There was no significant level of correlation between the two measures (Kendall's rank correlation coefficient, N=8, s=8, P=0,238).

FORAGING BEHAVIOUR

The location of the animal, as indicated by a section number on Figure 18 , provided the starting point for the statistical analysis of foraging behaviour. For each entry and transit through a section a number of variables relating to the foraging behaviour of the animal and the prevailing environmental conditions were quantified. The holt entered at the end of the foray, and the subsequent duration of the rest in that holt were also recorded.

To illustrate this presentation of the results a small section of this tabulation is reproduced in Table 24 . A full tabulation of the results is not presented as the unprocessed data are too extensive and unwieldy to be informative. The results of the statistical tests employed are given later.

The information recorded in the table refers to two separate forays by the animal and the subsequent rests in identified holts.

The animal's progress along the coast may be followed by reference to the section numbers and the map in Figure 18 . The distance covered in the respective sections is shown in column three in Table 24 . Where the animal traversed the entire section this distance was 500 m. In situations where the animal either entered the water from a holt located in the section or reversed its course while foraging in the section, as accurate an estimate as possible of the distance covered was made from the detailed radio-tracking data. When combined with the period of time spent in that section an estimate of speed through the water in that section was obtained.

A complete foray was recorded when the animal was tracked continuously between leaving one holt and entering another (or returning to the same holt). For these forays it was possible to record three further parameters

TABLE 24

Foraging behaviour of a radio-tracked male *Aonyx capensis* in the Tsitsikama Coastal National Park, 30/06/1982

Section number	Time foraging in section (min)	Distance covered in section (m)	Speed in section (m/10 (min)	Day or night	Tide state	Sea temperature °C	Sea conditions	Foray displacement (m)	Foray duration (min)	Foray speed (m/10 min)	Rest time (min)	Holt No.
51	10	150	150	N	L	15,8	3					
52	30	400	133	N	L-R	15,8	3	550	40	138	50	10
52	18	400	222	N	R	15,8	3					
51	72	600	83	N	R	15,8	3					
52	28	500	179	N	R	15,8	3					
53	12	200	167	N	R	15,8	3	300	130	154	558	7

namely foray displacement, foray duration and foray speed. Foray displacement is the distance between the holt vacated at the beginning of the foray and the holt occupied on completion of the foray. Thus if the animal returns to the same holt the foray displacement is recorded as 0 metres. Distance between holts is calculated according to the 500 m sections illustrated in Fig. 18 , and not simply the straight-line distance between holts.

It is important to stress that foray displacement and the distance covered in the course of the foray by the animal, from which foray speed is calculated, are not necessarily equal. Whenever an animal reverses its direction of movement during a foray, distance covered will exceed foray displacement.

Foray duration is simply the time spent on the foray. Foray speed is calculated using the distance covered in the course of the foray divided by the foray duration.

Column thirteen, Table 24 identifies the holt entered at the end of the foray (Fig. 18). Column twelve shows the time spent in that holt. Often the complete rest period was not recorded, the animal being abandoned by the observer before it emerged again from the holt. In those cases rest time was simply recorded as greater than the duration of holt occupancy at the time of abandonment; these data were not included in the statistical analysis.

The environmental conditions included in the statistical analysis are recorded in columns five, six, seven and eight of Table 24 . Column five identifies the foray as occurring during the day (D) or night (N). Sunrise and sunset were used as the thresholds between day and night, so that the twilight period at dawn and dusk is included in the night.

Column six gives the tide state during the foray; four tide states are recognised: rising (R), falling (F), high (H) and low (L). The tide cycle at Tsitsikama takes twelve hours twenty minutes, on average. Low tide is identified as a period one hour either side of the low tide time and high tide as a one hour period either side of the high tide time. Falling tide and rising tide occupy the remainder of the tide cycle. Tide times were obtained from the tide tables of the South African Hydrographic Office, Tokai.

Sea temperature has been obtained from the records of the weather station at Storms River Mouth. Only one temperature is used for each day; the mean of the two readings taken at 08h00 and 14h00. Sea temperature data were available for the complete duration of the radio-tracking study with the exception of August 1982 during which Dougal was being radio-tracked. This only affected one 24-hour radio track of Dougal.

Estimates of sea conditions are only available for the last otter to be radio-tracked, Dougal. Estimates of wind direction and speed were available from the weather records at Storms River Mouth, but these two parameters alone cannot provide a reliable indication of sea conditions. Therefore the measurement of sea conditions was based on a visual estimate made by the observer at the time of tracking, rated on a scale of one to ten. One corresponds to dead calm and ten to the worst sea conditions ever observed by the author in Tsitsikama. Dougal was never tracked in sea conditions heavier than eight on this scale.

A measure of average speed through a section was calculated from the figures in the fourth column of Table 24 , for two of the otters, Fat Freddy and Dougal. The speed of every foray by an animal in a particular section was recorded and the mean of these speeds calculated. A mean speed for an individual section was not calculated if less than three foray speeds had been recorded for that section.

TABLE 25

Mean foraging speeds of two radio-tracked male *Aonyx capensis* in specified 500 m sections of the Tsitsikama Coastal National Park. Study period: December 1981 - August 1982

Dougal

Section	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
Mean foraging speed (m/10 min)	212	263	183	366	142	122	119	125	225	277	167	73	140	141	183	123	93

Fat Freddy

Section	37	38	39	40	41	43	44	45	49	52
Mean foraging speed (m/10 min)	122	88	254	234	231	139	97	75	60	116

The rationale behind the calculation of these mean foraging speeds is that a lower foraging speed indicates more intensive foraging and possibly higher prey capture rate (see Discussion). On the basis of these figures it may be possible to identify the favoured hunting grounds of individual otters. The correlation between mean foray speed in a section and the frequency of radio fixes of each individual in that section was calculated (Fig. 20 , Range Utilisation Results).

STATISTICAL ANALYSIS OF FORAGING BEHAVIOUR

The greater part of this statistical analysis is confined to radio-tracking data collected for Fat Freddy and Dougal. Sample sizes for data collected on Biggles were small and hence statistical analysis of only some of these data was possible. Correlation coefficients between each of the three variables of a foray (displacement, duration and mean speed) and the duration of the subsequent rest (collectively known as the foray variables) were calculated from data collected during radio-tracking of Fat Freddy and Dougal. Initially these correlation coefficients were calculated from the combined data of all the animals radio-tracked. However it was found that this method sometimes obscured correlations in the data of individuals. All subsequent statistical tests were conducted on data pertaining to only one animal.

Of the twelve correlation coefficients calculated for the four foray variables listed above, only four were statistically significant. These were the positive correlations between mean foray speed and foray displacement for Fat Freddy (Spearman's Rank Correlation Coefficient: N=13, r_s = +0,696, P<0,01) and Dougal (Pearson's Correlation Coefficient: r_c = +0,345, 38 df, P<0,05), and between foray duration and foray displacement for Fat Freddy (Spearman's Rank Correlation Coefficient: N=15, r_s = +0,611, P<0,05) and Dougal (Pearson's Correlation Coefficient: r = +0,657, 41 df, P<0,001).

The four foray variables were tested for correlation with sea temperatures. Mean foray speed was negatively correlated with sea temperature for Fat Freddy (Spearman's Rank Correlation Coefficient: N=16, r_s = -0,725, P<0,01) and postively correlated for Dougal (Pearson's Correlation Coefficient: r_c = +0,904, 37 df, P<0,001).

Visual estimates of sea conditions were only available for the period of radio-tracking Dougal, so correlations between sea conditions and the four foray variables were only calculated for this animal. None of the correlations were statistically significant.

Variation in the foray displacements of Biggles, Fat Freddy and Dougal during the four different tide states was tested using the Kruskal-Wallis one way analysis of variance. No significant variation was found in any of the otters' foray displacements. Similarly no significant variation was found in mean foray speed of Fat Freddy and Dougal during the different tide states.

Foray duration was not tested against tide state, the proportion of total recorded foraging time being substituted. Biggles spent a higher proportion of time foraging at low tide, showed no bias during a falling tide, foraged less often on a rising tide and rarely at high tide ($\chi^2 = 150{,}37$, 3 df, $P<0{,}001$). Fat Freddy showed a strong preference for foraging at low tide, no bias during rising tide, limited avoidance of falling tide and strong avoidance of high tide ($\chi^2 = 43{,}10$, 3 df, $P<0{,}001$). Dougal reversed the major trend seen in Biggles and Fat Freddy showing a distinct preference for foraging at high tide, a marked avoidance of low tide and falling tide and a slight preference for a rising tide ($\chi^2 = 303{,}4$, 3 df, $P<0{,}001$).

The four foray variables were tested for significant correlation between day and night using the Mann-Whitney υ-Test. No significant day/night variation was found in any of the four variables for Biggles and Dougal. Fat Freddy, however, had a significantly slower mean foray speed during the day ($n_1 = 6$, $n_2 = 11$, $\upsilon = 8$, $p<0{,}02$) and significantly shorter rest times during the day ($n_1 = 4$, $n_2 = 7$, $\upsilon = 2$, $P=0{,}024$).

Fat Freddy displayed no significant day/night variation in foray duration or foray displacement.

The results of the tests on proportion of time spent foraging diurnally and nocturnally for Biggles, Fat Freddy and Dougal are recorded in the Results on activity pattern.

There was sufficient data for the calculation of mean foraging speeds of Fat Freddy in only nine of the sections of coast that he utilised (Table 25). Fat Freddy's mean foraging speeds were tested for correlation with the mean foraging speeds of Dougal in the same nine sections. Correlation was not significant at the 95% level (Kendall's rank correlation coefficient: N=9, S=16, P=0,06), but it was signficant at the 90% level.

There was a significant negative correlation between Dougal's utilisation of 17 sections and his mean foraging speed in those sections (Spearman's rank correlation coefficient, N=17, $r_s = -0{,}549$, $P<0{,}05$). There was no significant correlation between these two variables recorded for nine sections of Fat Freddy's range (Kendall's rank correlation coefficient: N=9, T=0,033, z=0,12, P=0,45).

OBSERVATIONS ON PREDATORY BEHAVIOUR

A striking feature of the predatory behaviour of Aonyx is that animals sometimes forage in cohesive groups. Two and sometimes three otters were seen to swim in close formation on the surface before diving, and often surfacing, simultaneously. This synchronised behaviour suggests that Aonyx sometimes hunts cooperatively.

The longevity of these foraging associations varied considerably (see Results), apparently because of variation in the otters' tendency to forage together. On some occasions groups were broken up by chance events (e.g. separation of otters by wave action). Yet on other occasions otters were seen to linger on the surface, the only apparent function of this behaviour being to maintain contact with a conspecific. As such observations were made on pairs of adult males, parental care could be ruled out as the motivation in these cases.

Though predation was frequently observed accurate quantification of this behaviour was only possible if the animal was hunting in a limited area. The usual mode of foraging was a steady progression along the coast and under these conditions only intermittent visual contact was possible.

The information collected relates to success rates for dives, duration of dives, handling time of prey, the proportions in which identified prey items were caught and the rate of prey capture during bouts of intensive foraging.

The success rate for foraging dives was estimated on the basis of observations on Fat Freddy and Dougal. Estimates for solitary animals and animals in a group are presented in Table 26 .

TABLE 26

Foraging success rates of Aonyx capensis hunting alone and in groups in the Tsitsikama Coastal National Park, December 1981 - August 1982

	Successful dives	Unsuccessful dives	% success	Sample size
Solitary otter	33	20	62,3	53
Otter in group	19	13	59,4	32

A test in the difference of success rates between animals foraging alone and animals foraging in a group revealed no significant difference (χ^2 = 0,002, 1 df, P > 0,9). The proportion of successful dives was almost equal for the two categories (62,3% for group foragers, 59,4% for solitary foragers).

The numbers of identified and unidentified prey items seen to be taken are recorded in Table 27.

TABLE 27

Numbers of prey caught during solitary and group foraging by Aonyx capensis in the Tsitsikama Coastal National Park, June 1981 - August 1982

		Unidentified prey	Fish	Crabs	Octopus
DOUGAL AND COMPANIONS	Group foraging	35	11	8	1
	Solitary foraging	64	13	9	0
ALL OTTERS	Solitary foraging	168	19	30	3

The proportions of fish and crabs taken by Dougal when solitary and by Dougal and his companions when foraging as a group were tested for a significant difference (χ^2 corr. = 0, 1 df, $P > 0,9$). The result shows these proportions as being very similar.

Similarly the proportions of fish and crabs taken by Dougal and his companions and all observed solitary foragers were compared. Again the result identifies no significant difference ($\chi^2 = 1,31$, with 1 df, $P > 0,10$).

Dougal was only tracked during the winter and other solitary foragers were observed throughout the year. A comparison of the proportions of fish and crabs caught by Dougal and all the other otters is shown in Table 28 below.

TABLE 28

Numbers of fish and crabs caught during solitary foraging by Dougal and other Cape clawless otters in the Tsitsikama Coastal National Park, June 1981 - August 1982

	Fish	Crabs
DOUGAL	13	9
OTHER OTTERS	6	21

The result of the test ($\chi^2_{corr.} = 5,55$, 1 df, $P < 0,05$) indicates a significant difference between the samples, Dougal catching proportionally more fish and fewer crabs. The size of these samples precludes basing firm conclusions on the results of the statistical tests.

The duration of 26 dives was recorded, eleven of them unsuccessful and 15 successful. Mean duration of unsuccessful dives was 23,6 seconds and of successful dives was 19,8 secs. The difference is not significant

(Mann-Whitney υ-test, $n_1 = 11$, $n_2 = 15$, $υ = 73$, $z = 0{,}493$, $P = 0{,}312$).

Handling time was recorded for 21 unidentified prey items, three crabs and six large fish. For the unidentified prey handling times were 3 - 480 s. (mean = 42,5 s., S.D. = 99,0). Handling times for the three relatively large crabs were 30 s., 32 s. and 180 s. The six large fish required handling times ranging from 180 - 900 s. (mean = 555 s.).

Rate of prey capture was recorded for 14 bouts of intensive foraging from one to nine minutes long. Rate of prey capture varied from 0,5 to 2,0 prey items per minute. A total of 75 prey items were caught in the recorded 65,5 min of intensive foraging, giving a mean rate of prey capture of 1,1 prey items per minute. Obviously this refers only to small prey items with a short handling time. Such intensive bursts of foraging occurred when the animal interrupted its progress along the coast to fish in a limited area. When the animal hunted while in transit the rate of prey capture was apparently much lower than during intensive bouts of foraging but it was not possible to quantify the difference.

SOCIAL ORGANIZATION

The majority of the information collected on the social organization of *Aonyx* on the Tsitsikama coast, was the result of the location and subsequent observation of animals made possible by radio-tracking.

Eric, Fat Freddy and Dougal were shown to share at least 8,5 km of coast on either side of Stormsriver. The re-capture of Eric and Oleg during the radio-tracking of Dougal and the sighting of both these animals in the company of Dougal was proof that occupation was simultaneous (not sequential) and that avoidance, which would indicate spatio-temporal territories for each animal, was not a feature of this social organization.

The known ranges of all the animals radio-tracked, plus that of Oleg who was followed in the company of Dougal on one occasion, are shown on the map in Fig. 14 . It would appear that otters from two more or less separate ranges were radio-tracked.

The holts used by more than one radio-tracked otter and the otters which shared these holts are listed in Table 29 . The location of these holts is shown on the map in Fig. 18.

TABLE 29

Holts used by more than one adult male *Aonyx capensis* radio-tracked in the Tsitsikama Coastal National Park, June 1981 - August 1982

Holts	19	18	33	9	8	11	13	5	4	1	6	10	7
Occupants	B, N	B, D, N	D, F	D, E	E, F	D, E, F	D, E, F	D, E, F	D, F	D, E, F	D, E	D, F	D, E, F

B=Biggles, D=Dougal, E=Eric, F=Fat Freddy, N=Naffer

Oleg, an adult male, had previously been trapped in holt 1, made use of this holt and certainly visited holts 5, 6 and 7 while in the company of Dougal.

An adult female was trapped at holt 5 on 18 July 1982 during the tracking period of Dougal. Another otter seen in the company of Dougal and Oleg on 13 August 1982 (13/8/82) and identified as a female or an immature male, may have been the trapped animal.

In the area west of the Geelhoutbos River, apart from the two resident males Naffer (died between 14th and 29th September 1981) and Biggles, an immature male and an adult female were trapped at the Geelhoutbos River (see map in Fig. 14) on 4/5/82 and 1/6/82 respectively (see Trapping Results).

Group sizes observed in the course of radio-tracking are shown in Table 30 , while those recorded incidentally are presented in Table 31. An indication of seasonal differences in group size is given in the tables.

TABLE 30

Group sizes of foraging *Aonyx capensis* observed during radio-tracking in the Tsitsikama Coastal National Park, June 1981 - August 1982

	Group size			
	1	2	3	4
October - March	16	0	0	0
April - September	28	8	4	1
All year	44	8	4	1

TABLE 31

Group sizes of foraging Aonyx capensis observed in the Tsitsikama Coastal National Park, February 1981 - August 1982

	Group size				
	1	2	3	4	5
October - March	23	3	6	3	1
April - September	19	9	2	0	0
All year	43	12	8	3	1

Only 21 of the sightings in Table 31 were made by the author. The remainder are confirmed sightings by Parks Board staff and visitors. One sighting of a solitary animal was not accurately dated and so is only included in the all year total.

Seasonal differences in group size were significant in both sets of results. In Table 30, radio-tracked animals sighted between October and March were invariably solitary whereas between April and September there were 13 sightings of the radio-tracked otter foraging with one or more companions ($\chi^2 = 4,77$, 1 df, $P < 0,05$).

There was a significant seasonal difference in the incidental sightings too, there being a higher proportion of pairs in April to September and a higher proportion of groups of three or more otters in October to March ($\chi^2 = 8,225$, 2 df, $P < 0,01$).

There was no significant difference between the year totals of group sizes for the two categories of sightings ($\chi^2 = 2,89$, 2 df, $P > 0,10$). There is however a significant difference between the October - March distribution of group sizes for the two categories ($\chi^2 = 5,90$, 1 df, $P < 0,05$), again due to the lack of anything but solitary sightings during radio-tracking in this period. There is no significant difference between the April to September sightings for the two categories ($\chi^2_{corr.}$ = 0,042, with 1 df, P > 0,50).

The cohesiveness of the foraging groups followed during radio-tracking did not appear to be very high, formation and dispersion of such groups seeming to be largely a matter of chance. An encounter leading to formation of a group might take place in the sea (observed on one occasion) or in a holt (at least one occasion). Dispersal of a foraging group was recorded twice in the sea and possibly once by staggered departure from a holt. It was not known in the latter case whether or not the two animals sharing the holt were aware of each other but it seems likely that they were.

The longevity of these foraging associations varied considerably, some lasting minutes while others apparently lasted days. On one occasion Eric was seen to enter a holt alone to emerge five hours later in the company of a smaller otter. The pair foraged together for only ten minutes before separating. In contrast Dougal and Oleg were once seen to commence foraging together at sunset and were still foraging together three hours after sunrise the next day. Vocalizations heard throughout the night suggested that they had remained together.

Two incidents involving groups of otters have considerable implications for the social organization.

The first incident was observed during the foray of Dougal and Oleg mentioned above. The otters were hunting together in a small gully, diving and surfacing in synchrony. After a series of such dives they surfaced simultaneously, Oleg in possession of an octopus and Dougal without a prey item. Oleg climbed onto a rock to handle the octopus, followed closely by Dougal. After Oleg had commenced eating Dougal extended a fore-paw, appropriated a substantial portion of the octopus and settled down to eat it. There was no aggressive interaction at all, Oleg merely continuing to eat the remaining part of the octopus and ignoring Dougal.

Two mature males sharing a prey item that had been caught by only one of them is remarkable behaviour in that it is apparently altruistic.

Only one incidence of intraspecific aggression was recorded during the study, and this by a visitor to the Park, not the author. Two otters were seen to attack a third in the water immediately outside holt 1 near Stormsriver mouth (ig. 18), injuring the lone animal severely. The fight ended when the injured animal left the water and retreated into the bush in the vicinity of holt 1.

DISCUSSION AND CONCLUSIONS

COASTAL SURVEY - ASSESSMENT OF HOLT UTILISATION

The validity of using the occurrence of otter sign at a site (Table 4) as a measure of utilisation of that site depends on the assumption that the ratio of visits : occurrence of sign is constant for all sites monitored. The only support for this assumption is van der Zee's (1979) finding that there is good correlation between the presence of an otter at a holt and occurrence of fresh otter sign there. However this conclusion was based on a sample of only 28 sightings at seven holts, so the assumption is by no means proven.

The number of spraints found at each holt provides a more comprehensive record of utilisation as a substrate suitable for the retention of tracks was present at only three of the ten sites surveyed. The occurrence of tracks does not contribute to the final assessment of levels of utilisation.

The wide variation in the total number of spraints found at each site (e.g. 4 spraints at holt 34 compared to 64 spraints at holt 7, see Figure 18 for location of holts) suggests that there is a wide variation in the frequency of utilisation of different holts. Radio-tracking of the three adult males Eric, Fat Freddy and Dougal supports this conclusion. Holt 7 was used regularly by all three otters throughout the period of radio-tracking, whereas holt 34 was used infrequently by only one of the three, Dougal. The radio-tracking results appear to be in close agreement with the coastal survey results if conclusions are based on the data for these two holts alone. However correlation between these two methods of recording utilisation rates of holts was tested for a total of eight holts lying between Steilkop and George se baai (Fig. 6) and no significant correlation existed (see Holt Utilisation Results).

Temporal variation in the occurrence of spraints at holts 4, 6, 7 and 12 is illustrated in Figure 5 . All these holts display a wide variation in the numbers of spraints deposited per day and presumably therefore in the levels of utilisation. It appears that despite these wide fluctuations, the relative levels of utilisation of some holts display a consistent relationship. Figure 5 indicates that holt 7 is consistently used more often than holt 6 which in turn is used more often than holt 12. However this relationship may only have applied during the four months of the survey.

The variation in the number of spraints deposited at holt 4 reverses the trend seen in the other three holts. There is a significant negative correlation between the number of spraints per day at holt 4 and the total number of spraints per day found at holts 6, 7 and 12 (see Results). Such a relationship is to be expected if the overall utilisation of the whole 6 km stretch of coast has remained unchanged. In this situation when the rate of utilisation of some holts declines, that of others within the same area will increase unless the local otter population has decreased.

Irregular observations made during the remainder of the study appeared to confirm the pattern of utilisation illustrated in figure Fresh otter sign was absent from known holts for extended periods (sometimes up to a month). Then, in the course of a few days, a large number of fresh spraints would appear and regular use might continue for several weeks thereafter. For example a site at the

Waterfall River (Fig. 6) was not used for two months and then in the space of two to three days 14 fresh spraints appeared there. The site fell into disuse again immediately thereafter.

The only other detailed study of spatial and temporal variation in the occurrence of spraints in a coastal population of otters is that of van der Zee (1979) on *Aonyx*. Less detailed studies on the spacing of holts and spraint sites in coastal populations of the European otter, *Lutra lutra*, have been conducted by Kruuk & Hewson (1978), Watson (1978), Macdonald & Mason (1980) and in a riverine population by Jenkins & Burrows (1980). Only limited data on the variation in levels of utilisation were provided (see later).

Van der Zee (1979) describes a similar pattern of holt utilisation to that observed during the present study. He noted both wide temporal variation in the use of individual holts and variation in mean percentage utilisation between holts. Van der Zee suggested that, on the basis of the latter variation, holts might be classified as main or subsidiary holts. These terms were first suggested by Kruuk & Hewson (1978) for holts in a coastal population of *Lutra lutra* in Scotland. However the distinction in *Aonyx* is by no means as clear cut as it is in *Lutra lutra*. Furthermore the existing data suggests that there are major differences in social organization between *Aonyx* in Tsitsikama and *L. lutra* on the Scottish coast. This will presumably result in significant interspecific differences in holt utilisation. Definitions of main and subsidiary holts are therefore likely to differ considerably even if they were applicable to *Aonyx*.

FACTORS AFFECTING HOLT UTILISATION

Spatial variation in holt utilisation seen in Aonyx may be related to foraging behaviour. Those holts with a higher mean utilisation rate may be in the vicinity of favoured feeding grounds. Some observations made in the course of radio-tracking tended to support this hypothesis, and statistical analysis of radio-tracking data provided limited proof.

Temporal variation in holt utilisation may also be linked to the exploitation of local prey populations. Repeated use of one holt and adjacent fishing areas is likely to lead to depletion of prey stocks on a local scale. Less mobile prey species such as Plagusia chabrus and Octopus granulatus are particularly prone to local variations in population density produced by fluctuations in predation pressure. This could lead to the observed pattern of holt utilisation in which periods of intense usage alternate with periods of relative disuse.

Resumption of occupancy of individual holts after a period of disuse may be linked to social behaviour. An established holt that is abandoned by the residents might be occupied by residents of the neighbouring range or transients. Less favoured holts may therefore be occupied at regular intervals merely to maintain ownership, both by physical presence and deposition of spraints or other signals (e.g. anal gland secretions). Otters may visit a holt merely to deposit spraints or scent without actually entering and occupying the holt. Observations made in the course of radio-tracking appear to support this suggestion (see Discussion on radio-tracking results).

Finally patterns of holt utilisation may be linked to individual differences in the use of holts by clan members. Radio-tracking data suggest that some holts are only used by one or two members of a clan. Thus if the behaviour of only one animal changes (e.g. the animal starts to forage in company or shifts its centre of activity) a holt will fall into disuse. This would also provide an explanation for the consistently lower utilisation rates of some holts. A holt used by all or most of the clan members will presumably exhibit consistently higher numbers of spraints than a holt regularly used by only one or two clan members.

HOLT AND SPRAINT DENSITIES

Reference to Figure 6 and Table 5 provides a detailed analysis of the variation in holt and spraint densities recorded on different sections of the Tsitsikama coast. Spraint densities vary between 21,5 spraints per km (straight-line distance of coast) and 67,8 per km. Holt densities vary between 0,97 holts per km and 3,06 holts per km.

These variations in holt and spraint density can be partially explained by topographical differences in the coast. The section of coast with the lowest holt and spraint densities consisted largely of sheer cliffs with only occasional interruptions by kloofs and small bays. As a result the availability of suitable holt sites was limited. Nowhere else in the Park was availability of holt sites deemed a limiting factor. This contrasts sharply with the situation in the Shetlands, where Watson (1978) suggested that there was a dearth of suitable sites for holts for a coastal population of Lutra lutra.

In the remainder of the Park differences in holt and spraint density may have reflected differences in the population density of Aonyx.

There is evidence to suggest that relative spraint densities provide an accurate indication of relative population. This rests on the assumption that the density estimates obtained using the ^{65}Zn technique (see Population estimate - results) are accurate. These estimates for the two sections of coast studied were in close agreement - one otter per 1,85 km coast between Elands and Eerste rivers and one otter per 2,0 km of coast between the Elandsbos River and Rietmondjie (Fig. 9). The respective spraint densities for these sections of coast recorded during the coastal survey were 51,6 spraints per km and 48,2 spraints per km (Table 6). The ^{65}Zn estimate suggests that the density of otters is 8% higher in the eastern section, spraint densities suggest that it is 7% higher in the eastern section - a very close agreement. However both estimates depend ultimately on spraints and a common error cannot be ruled out.

If relative spraint densities are an accurate measure of relative otter densities then it would appear that the density of otters is somewhat lower west of the Witels River (Fig. 6) than it is in the remainder of the Park. It would, however, be inappropriate to base any firm conclusions on only one survey of spraint and holt densities, particularly as a thorough survey of the section between the Klip River and the Groot River at Nature's Valley (Fig. 6) was impossible (see Results section).

Though the mean holt densities east and west of Stormsriver do not differ significantly there is a significantly higher density of spraints east of Stormsriver. This is in part due to the low density of holts west of the Bloukrans (Fig. 6).

It is not clear what this difference in spraint density signifies. The strong correlation between spraint densities and holt densities (see Results) suggests that the level of utilisation of holts does not differ east and west of Stormsriver. Higher spraint density with similar levels of holt utilisation might indicate more otters east of Stormsriver. This is refuted to some extent by the intrinsically more reliable ^{65}Zn population estimate. This indicates more or less equal population densities on sections of the coast west and east of Stormsriver.

Though there is no significant difference, Van der Zee (1979) suggested that holt densities are higher to the east of Stormsriver and could be linked with the higher density of freshwater streams and pools. Despite the fact that not all holts found were directly associated with fresh water, the presence of a nearby freshwater supply was undoubtedly one of the main factors determining the location of holts. The slightly higher density of holts may simply be a response to a slightly higher density of streams and freshwater pools. Assuming that a freshwater drinking supply is one of the major requirements at a holt, such a hypothesis is plausible if Aonyx establishes holts at all the suitable sites. This is discussed further, below.

HOLT DISTRIBUTION

The selection of holt sites may be based on a simple strategy of minimising inter-holt distances. This would have the effect of reducing energy expenditure during foraging trips by reducing the distance between foraging areas and holts. Such a strategy is plausible in view of the rudimentary nature of the holts, usually only a shallow scrape under a bush. This ensures that little effort is required to establish a holt and plenty of suitable sites are available. As the social organisation of Aonyx in Tsitsikama (see relevant Discussion and Conclusions) does not confine the animal to a single main holt, such behaviour is possible. This may not be the case with other species such as Lutra lutra (Kruuk & Hewson, 1978).

Circumstantial evidence for this strategy is to be found in a comparison of the length of forays made by Aonyx as compared to the distribution of nearest neighbour distances (Fig. 7). In a sample of 78 forays recorded during radio-tracking, the mean displacement along the coast was 676 m, the longest recorded displacement in the course of one foray being 3600 m. The mean nearest neighbour distance between holts is only 350 m, approximately half the average displacement. This contrasts sharply with the behaviour of Lutra lutra on the Ardnish peninsular in Scotland. Here the mean nearest neighbour distance between holts is 1160 m (Kruuk & Hewson, 1978) and animals may have to travel up to 700 m to reach their foraging areas. The animal will often return to the original holt at the end of the foray. Backtracking appeared to be less frequent in Aonyx and though the longest reversal of course recorded was 750 m, the mean (n=17) was only 250 m.

Examination of the distribution of nearest neighbour distances between holts on the Tsitsikama coast (Fig. 7) indicates that neighbouring holts are more evenly spaced than could be expected if the holts were distributed at random. Comparison between the observed distribution and a random distribution of nearest neighbour distances, generated by using the Poisson expansion, indicates that there are fewer closely spaced (< 200 m) and widely spaced (> 500 m) holts in the observed distribution ($\chi^2 = 33{,}09$, with 6 df, $P < 0{,}001$).

At first sight the absence of closely spaced holts appears to refute the hypothesis that Aonyx is tending to minimise inter-holt distance. However there must come a point at which further proliferation of holts serves no useful purpose, especially if fresh water is usually a prerequisite. It benefits an otter to travel a further 100-150 m to a holt with a supply of fresh water, rather than establish a new holt at a site lacking fresh water.

This pattern of holt distribution is similar in some respects to that found by Kruuk & Hewson (1978) in a coastal population of *Lutra lutra*. Their small sample (n=9) indicated that there were fewer closely spaced holts than expected for a random distribution. However there was no indication that there were fewer widely spaced holts. The mean nearest neighbour distance was much higher, 1160 m as compared to 350 m for the *Aonyx* population in the present study. Macdonald & Mason (1980) did not give a mean nearest neighbour distance for another coastal population of *Lutra lutra* in Scotland; however the mean inter-holt distance was 1100 m, the same as that calculated by Kruuk & Hewson (1978). This compares with a mean inter-holt distance of 470 m for the 116 holts included in the analysis of holt distribution in *Aonyx*.

Watson (1978) working on *Lutra lutra* in the Shetlands gave no estimates for mean inter-holt or mean nearest neighbour distances. Examination of the mapped holts indicates that they occurred in closely associated pairs, widely separated from the neighbouring pair. Paired holts were sometimes only 100 m apart while neighbouring pairs of holts were up to 2500 m apart.

These differences in holt distribution presumably reflect the observed differences in the social organisation of coastal populations of *L. lutra* and *Aonyx*. Watson (1978) found that adult females largely restricted their activities to one or two holts. Kruuk & Hewson (1978) also suggested that individual otters or groups of otters (possibly family groups) occupy only one main holt and any associated subsidiary holts. Furthermore there was no evidence for a clan system of social organization in the Shetlands. In contrast individual otters in Tsitsikama were known to use as many as 19 holts (Table 22) and groups of adult males occupied a clan range and foraged together (see Results).

Comparison of population densities leads to the rather startling conclusion that a higher density of L.lutra is accompanied by a far lower density of holts. The minimum density of L. lutra studied by Kruuk & Hewson (1978) was in the region of one otter per 1,2 km of coast while the estimate for Aonyx in Tsitsikama is one otter per 1,9 km. This corresponds to mean inter-holt distances of 1100 m and 470 m respectively. It appears then that Aonyx at approximately two thirds of the population density of L. lutra, use more than twice as many holts per km of coastline.

Patterns of holt utilisation and distribution are related to social behaviour, and differences in the latter have been shown to be related to differences in the distribution of an animal's food supply (Kruuk 1975). Explanation of the differences in holt utilisation and distribution of Aonyx and Lutra is therefore likely to require investigation of these otters' prey species, and the habitat in which they forage.

DISTRIBUTION OF SPRAINT SITES

The distribution of all spraint sites, comprising of between one and 52 spraints, in relation to the nearest holt is illustrated in Figure 8 . The concentration of spraint sites in the vicinity of holts is immediately apparent. Sites less than 50 m from a holt have been established by those animals using the holt as they leave or enter it.

In fact some of the spraint sites which are between 50-100 m from a holt are directly associated with that holt. The spraint site at a holt tended to be close to the water's edge even if the holt itself lay some distance from the sea.

The concentration of spraints close to holts is even more marked if one considers the proportion of the total number of spraints that are deposited here. 85,4% of the spraints were found in the spraint sites at holts. The remainder were scattered singly and in small groups (usually < 10) at intervals between the holts.

Macdonald & Mason (1980) studying the marking behaviour of a coastal population of Lutra lutra, identified four main types of spraint sites. The categories they defined are applicable to the distribution of spraints found in Tsitsikama. The first category, large accumulations found at the entrances to holts, contains the vast majority (85,4%) of spraints found on the Tsitsikama coast. The second category, that Macdonald & Mason called "lavatories", made up only a small proportion of the sites in Tsitsikama. These are large accumulations not at the entrances to holts. Only seven such sites were found, containing 4,4% of all the spraints found in the coastal survey (see Results). These lavatories are marked as spraint sites on the map in Figure 6 . The third cateogry was small accumulations (2-10) of spraints and the fourth was single spraints. These two categories accounted for the remaining spraints found (see Results).

Comparison of the results shown in Figure 8 with the results obtained for Lutra lutra by Kruuk & Hewson (1978) and Macdonald & Mason (1980) reveals that the concentration of spraint sites at holts is more pronounced in Aonyx than in L. lutra. 56,2% of spraint sites are less than 50 m from holts in the Tsitsikama population of Aonyx, compared to 44% for the Ardnish population of L. lutra (Kruuk & Hewson, 1978) and 24% for the Loch Broom population of L. lutra (Macdonald & Mason, 1980). Only 20,3% of spraint sites were further than 150 m from a holt in Tsitsikama, compared to 40% in Ardnish and 38% in Loch Broom.

The main reason for the observed differences is likely to be the much lower inter-holt distances in Tsitsikama (see above). Aonyx may travel overland less frequently or come ashore between holts less often than L. lutra, but the variation in inter-holt distances alone is probably a sufficient explanation.

The higher frequency of utilisation of sites closer to the holts is probably due to more frequent visits. Six of the seven lavatories that were found were located on well used runways, ensuring frequent visits from otters. This accounts for the large accumulations of spraints away from holts. The reason for the establishment of the seventh lavatory, just west of the Klip River (Fig. 6), is not apparent.

FUNCTION OF SPRAINT SITES

Defecation in Aonyx can be classified as a form of scent-marking as it serves to dispense the odour of the defecating animal (Kleiman 1966). The use of faeces as a scent mark is widespread among carnivores some examples being the maned wolf, Chrysocyon brachyurus (Kleiman 1972), the spotted hyaena, Crocuta crocuta (Kruuk 1972), the European badger, Meles meles (Kruuk 1978) and the golden jackal, Canis aureus (Macdonald 1980).

Johnson (1973) pointed out that scent-marks could fulfil a variety of functions. As it was not possible to make detailed observations of the behavioural response of Aonyx to spraints, the only clues we have to the function of spraint sites is the distribution of the sites themselves.

Unfortunately the fact that spraints are concentrated at holts is not particularly informative. Aonyx can only establish spraint sites ashore, and as most of their time ashore is spent in holts it is therefore not surprising that most of their spraints are deposited close to holts (Fig. 8). It is probable that the liberal marking of well-used sites and the scattered marking of the remainder of the coast merely serves to maximise the encounters of conspecifics with an animal's scent. Whatever the signal conveyed by the spraints this is the expected strategy if they are to convey a message to a conspecific.

The only other possible clue to the function of the spraints is the function of spraints in other otter species. This has only been investigated by Erlinge (1968) in Lutra lutra. Working on L. lutra in a freshwater habitat in Sweden, Erlinge found that intense sprainting occurred in the meeting zones of otters coming from different areas. He deduced from tracks that family groups often travelled to the boundary zone, sprainted, and then returned to the centre of their range (Erlinge 1967b). Furthermore at times of high population density otters increased their signalling activity. These observations suggest that spraints have a territorial significance in Lutra lutra.

Gorman, Jenkins & Harper (1978) were able to show that the anal sac secretions of Lutra lutra have a sexual significance. Females secreted only during oestrus and if accompanied by a male, the male showed synchronous bouts of secretion. As Erlinge (1968) found no indication of sexual significance it would appear that *Lutra lutra* has a two-tier marking system - spraints for territorial marking and anal sac secretions for sexual attraction.

At the spraint sites of *Aonyx* in Tsitsikama, small deposits of a green, jelly-like substance with a musky smell were occasionally found amongst the spraints. It seems likely that these were anal sac secretions, especially as they resemble those of *Lutra lutra* (pers. obs.). The fact that they occurred at irregular intervals and far less frequently than spraints suggests that the function of these secretions is different from that of the spraints.

So it would appear that *Aonyx* may also employ different scent-marks to convey different signals. There is no proof that the significance of the two scent-marks is similar to that in *L. lutra*. All that can be said is that the fact that the spraints of *Aonyx* are not concentrated at the borders between clan ranges, does not rule out a territorial significance for the spraints. Macdonald (1980) noted that middens, (for *Aonyx* read spraint sites), close to the lair are common among communally denning animals. Peripheral middens are only found in clan dwellers defending a relatively small territory. Peters & Mech (1975) found that wolves, *Canis lupus*, with large territories did not mark the boundaries and surmised that this was due to the effort required. With such a large territory, the wolves would spend the majority of their time marking the widely separated boundaries. In *Aonyx* range limits may be separated by as much as 19 km of coast (radio-tracking results) due to the linear nature of the habitat. In this situation marking sites within the range at points where encounters with intruders are likely incurs a much lower energetic cost. The wolves studied by Peters & Mech (1975) marked the trails and especially the trail junctions within their ranges. *Aonyx* marks the holts.

FEEDING ECOLOGY

Otters between the Bloukrans and Geelhoutbos rivers were catching a much higher proportion of fish and lower proportion of crabs than the otters inhabiting the coast between the Kleinbos River and Steilkop. One cannot therefore generalise about the diet of Aonyx on the basis of studies carried out in limited areas.

The economics of foraging strategies will vary in areas in which otters have differing diets. Two of the factors involved are the mobility and calorific content of the prey. In the case of the fish and crabs hunted by Aonyx these two factors tend to balance the profitability (net energy gain divided by handling time, Krebs, 1978) of the prey. Fish are more mobile and are therefore likely to require more energy expenditure during pursuit and capture, reducing prey profitability. However crabs have a lower calorific content and also a smaller proportion of assimilable biomass than fish, reducing net energy gain.

To the calorific values listed in the results can be added values for the red rock crab, Plagusia chabrus (10,80 kJg^{-1} dry mass) and a fish Clinus superciliosus (17,60 kJg^{-1} dry mass) determined by Field et al. (1980). Thus the two crab species preyed upon by Aonyx on the Tsitsikama coast have calorific values of 10,7 kJg^{-1} dry mass (Cyclograpsus punctatus) and 10,8 kJg^{-1} dry mass (Plagusia chabrus). Three fish preyed upon by Aonyx have calorific values ranging from 17,60 kJg^{-1} dry mass (Clinus superciliosus) to 22,0 kJg^{-1} dry mass (Clinus cottoides). For the purposes of this discussion the calorific values of these three fish species are used as an approximation of the calorific values of other fish species in the diet of Aonyx. The majority of fish taken by Aonyx are of similar size and morphology and some are close relatives of the three species for which calorific values are known.

Examination of Table 1 , adapted from van der Zee (1979) indicates that indigestible hard parts form a much larger proportion of crab biomass than fish biomass. Thus both the assimilable proportion and the overall calorific value of the two crab species are lower than those of three of the most important fish species in the diet of Aonyx.

Examination of Table 9 indicates that fish account for 43,6% of the estimated live mass of prey consumed by otters between the Bloukrans and Geelhoutbos rivers. This compares with only 28,4% fish in the estimated live mass of prey consumed by otters between the Kleinbos River and Steilkop. Live mass estimates of both species of crab are 40,7% and 57,3% in the Bloukrans-Geelhoutbos River section and Kleinbos River - Steilkop section respectively. The estimated percentage live mass of Octopus granulatus consumed on the two sections of coast is similar.

In terms of calorific value fish species will provide a far higher proportion of the otters' energy requirements than crabs between the Bloukrans and Geelhoutbos. Between the Kleinbos River and Steilkop it appears that fish will provide at least as much of the energy requirements as crabs. The estimated percentage live mass of crabs consumed is twice that of fish in this section but calorific value of the fish is appreciably higher than that of crabs (see above) and a far higher proportion of the former is assimilable.

It is not clear whether this difference in prey composition is due to local variations in prey availability or differences in the foraging strategies of otters in the two areas. Crabs and fish may in fact be of similar profitability as the former have a lower calorific content but the latter are more mobile. In this case specialising on crabs might simply be an alternative strategy to specialising on fish, with similar overall profitabilities accruing to animals adopting either strategy.

The increase in the proportion of fish in the diet between the Bloukrans and Geelhoutbos rivers compared with the section between the Kleinbos River and Steilkop is accompanied by a significant change in the proportions of the four most frequently taken species or taxa, *Cheilodactylus fasciatus*, *Chirodactylus brachydactylus* and clinids constitute a higher proportion of estimated fish live mass in the diet between the Bloukrans and Geelhoutbos rivers (Table 8). *Chorisochismus dentex* contributes 58% of fish live mass to the diet of *Aonyx* in the section between the Kleinbos River and Steilkop; but only 41% of the fish live mass between the Bloukrans and Geelhoutbos rivers. However the same two species and one family predominate in both areas; *Chorisochismus dentex* *Cheilodactylus fasciatus* and clinids. These three taxa account for 87,8% of consumed fish live mass between the Bloukrans and Geelhoutbos rivers and 81,6% between the Kleinbos River and Steilkop. The greater proportion of fish in the diet of otters in the former area is largely due to the increase in numbers of these three taxa in the diet.

There is no significant variation in the frequency distributions of size classes of *Plagusia chabrus* or *Chorisochismus dentex* between the two sampled areas. Therefore the populations of the two species in the different areas have similar distributions of size classes or, if the prey populations differ, *Aonyx* is consistent in its selection of size classes. Similarly, the absence of temporal variation in the size class frequency distributions does not necessarily imply that the composition of prey populations in terms of size classes has remained unchanged between 1977-1978 and 1982.

The dramatic increase in the proportion of *Cheilodactylus fasciatus* in the diet and decrease in *Chirodactylus brachydactylus* is difficult to explain unless one assumes that there has been a similar variation in the population sizes, or at least the availability, of these two species between 1977 and 1982. Aonyx is unlikely to display such a dramatic shift in prey selectivity over a period of only five years. This is the only other possible explanation if the availability of these two prey species has remained more or less constant.

TRAPPING

The location of trap sites and other points referred to in this discussion may be found on the map in Fig. 6 .

There was considerable variation in trapping success between different sites (Table 11). The trap rate ranged from 0% (for eight trap nights at Blue Rocks) to 66,7% (for six trap nights at holt 18). This variation is deemed to be attributable to three main factors: (i) the local density of otters; (ii) the frequency with which the trap site was used by otters, and (iii) the wariness of the local otters.

In Table 12 the trap rates for different sites are combined and placed in three broad categories on the basis of variation in these three factors. The very high trap rate (37,5%) obtained within the Park boundaries but outside the rest camp is probably due to a relatively high density of otters (estimated as one animal per 1,9 km of coast) and reduced wariness due to the protection afforded by National Park status.

In the rest camp and immediate vicinity the local population density and utilisation is probably similar to that in the rest of the National Park. Evidence for this is that spraint densities recorded during the coastal survey are similar inside (52 spraints per km) and outside the rest camp (47,3 spraints per km). A reasonable explanation for the difference in trap rate between these areas would seem to be that the otters are more wary around the rest camp with its high levels of human activity.

Outside the Park the low trap rate (6,3%) is probably due to both increased wariness due to greater human activity and a lower otter density. The evidence for a lower otter density in the vicinity of

Blue Rocks and Salt River is the much lower spraint density there. A survey of this area in January 1982 revealed a spraint density of approximately 10,3 spraints km^{-1}, compared to 47,5 spraints km^{-1}. The trap rate within the Park boundaries was 18,6%.

An indication of the importance of utilisation of a site in determining trap rate was provided by the results obtained at site number 5 near the Geelhoutbos (Fig. 6). There are no exact figures on utilization for this site. However on the basis of otter sign (tracks and spraints) found during repeated visits, this appeared to be the most heavily and consistently utilised holt known to the observer. It also yielded the highest trap rate: 66,7% for six nights trapping.

Thus it would appear that for a given population density of Aonyx, trap rate can be maximised by concentrating on the areas most heavily utilised by otters and least utilised by humans. The limited evidence suggests that these areas probably coincide in the Tsitsikama.

The overall trap rate of 16,7% (102 trap nights) compares favourably with previous attempts to trap otters. Van der Zee (1979) achieved an overall trap rate of 8,3% with a standard caracal trap. However he confined the use of these traps to the rest camp and immediate vicinity, and used a light-weight trap, with a success rate of only 2%, in the more remote parts of the Park.

Though inland populations of Aonyx are trappable, communications from various conservation officers working for provincial bodies indicate that they are not as easily caught as the Tsitsikama population.

The trap rate achieved is much higher than that achieved using stationary traps for other otter species. Loughlin (1980) captured

24 sea otters (*Enhydra lutris*) over a period of 20 months using specially developed hand-held traps. However no assessment of trapping success is given. Northcott & Slade (1976) achieved a trap rate of 1,3% using Hancock traps for *Lutra canadensis* in a marine habitat. This trap rate was only achieved after extensive modifications to the technique used.

Lutra lutra, the European otter, appears, if anything, to be even less trappable than *Lutra canadensis*. Dunstone (*pers. comm.*) has indicated that *Lutra lutra* in mainland Britain is more or less untrappable. However the population in the Outer Hebrides and the Shetlands (Kruuk, *pers. comm.*) may ultimately prove susceptible to refined trapping techniques.

SEX RATIO

The trapping data from both Tsitsikama studies on first inspection tends to suggest that the sex ratio may not be 1:1. However a χ^2-test, corrected for continuity (Parker, 1979) reveals that neither van der Zee's trapping ratio of 7 males : 2 females (χ^2 = 1,77 with 1 df, $P > 0{,}1$) nor the ratio of 8 males : 4 females (χ^2 = 0,75 with 1 df, $P > 0{,}1$) obtained in the present study, differ significantly from that expected if the sex ratio were 1:1. Even with the trapping data of the two studies combined, giving a ratio of 15 males : 6 females, there is no significant deviation from an expected 1:1 ratio (χ^2 = 3,05, with 1 df, $P > 0{,}05$).

Even if a significant deviation existed in the sex ratio of trapped animals it would not necessarily be an accurate estimate of the sex ratio in the population at large. It might reflect only a difference in the trappability of the two sexes. There is some evidence pointing to a sex-linked variation in trappability. In several cases, tracks around empty traps revealed that the trap had been inspected but not entered by groups of otters consisting of one adult and one or more immatures. It seems safe to assume that the adult was a female. Increased wariness in females accompanied by offspring seems likely to confer a selective advantage on those females, so that this behavioural response certainly appears plausible in evolutionary terms.

DIMENSIONS AND BODY MASS

Table 32 is essentially reproduced from van der Zee (1979) with the addition of data collected in the present study. Comparison of the Tsitsikama data reveals that there is no difference in the mean mass of females (12,4 kg) caught during the two studies and that though there is a difference in the mean mass of males caught (13,6 kg in the present study *cf.* 13,1 kg in van der Zee's study) it is not statistically significant (Student's t-test, $t = 0,383$, 13 df, $P > 0,90$). This is not unexpected as van der Zee's study was conducted only four years before the present one and there has been no apparent change in the environmental conditions in Tsitsikama in the intervening period.

When the data from the two Tsitsikama studies is pooled, mean mass of males is 13,4 kg (n=15) and mean mass of females is 12,4 kg (n=6). This compares with mean mass of inland otters, taken from the three localities shown in Table 32, of 13,3 kg (n=13) for males and 13,5 kg (n=5) for females. The mean masses of males for inland and coastal areas are almost equal while the 0,9 kg difference in the mean mass of females is not statistically significant

TABLE 32

Dimensions of Cape clawless otters caught in the Tsitsikama Coastal National Park and elsewhere in southern Africa

	Tsitsikama Coastal National Park (present study)		Tsitsikama Coastal National Park (van der Zee, 1979)		King William's Town District		Transvaal		Zimbabwe	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
Total length (mm)		(n=3)								
Mean ± S.D.	1262± 113,9	1245± 65,7	1216± 52,1	1215± 72,5	1328	1343	1240	1259	1313	1570
Range	1008-1380	1170-1330	1130-1280	1145-1285	1260-1420	1245-1440	1235-1244	1168-1350	1100-1800	1170-1970
Tail length (mm)		(n=3)								
Mean ± S.D.	479± 39,0	465± 17,8	512± 32,7	488± 7,5	525	578	476	453	501	530
Range	405-530	450-490	475-570	480-495	470-570	485-670	475-476	431-475	443-540	
Weight (kg)										
Mean ± S.D.	13,6± 2,37	12,4± 1,11	13,1± 2,32	12,4± 0,65	17,5 (n=2)	15 (n=1)	13,3	12	12,3	14,3
Range	8,9-17,7	11,0-13,8	10,0-16,4	11,7-13,0	16,8-18,2		9,5-17,0	12-12	10,0-15,4	12,3-16,3
Sample size (n)	8	4	7	2	7	2	2	2	9	2

S.D. given where available

(Student's t-test: $t = 0,904$, 6 df, $P > 0,1$).

Bearing in mind that the sample sizes are small there appears to be no significant difference in the mean mass of otters from inland and coastal populations. It may however be that the largest inland otters attain a greater size than the largest coastal otters. Smithers (1979) measured an 1800 mm male in Zimbabwe, 420 mm longer than the largest otter measured in the Tsitsikama (Table 32). However the only reliable record of an otter exceeding the weight of the heaviest Tsitsikama otter (17,8 kg) is of an 18,2 kg male from King William's Town (van der Zee, 1979).

The data on recaptures provide evidence on the status (i.e. transient or resident) of some of the otters. It seems reasonable to assume that any animal caught more than once in the same area is resident. Limited confirmation of this assumption is provided by radio-tracking data.

The animals recaptured were otter 1 (male, Oleg), otter 2 (male Eric), otter 5 (male, Fat Freddy) and otter 7 (male, Dougal).

Otter 1 was caught twice, with an interval of 14 months between captures. His residential status is apparently confirmed by a subsequent sighting of this animal foraging between Steilkop and Rietmondjie in the company of another resident male (Fig. 14).

Otter 2, Eric, was captured twice, almost 13 months elapsing between capture and recapture. Residential status is confirmed by radio-tracking over a three week period during which he was located fifteen times between Skildekrans and Steilkop (Fig. 14). The animal was also seen in the company of Dougal (otter 7) in the vicinity of holt 1 (Fig. 18).

Otter 5, Fat Freddy, was captured twice, with an interval of almost three months between capture and recapture. Fat Freddy was radio-tracked over a period of five weeks and was located on every radio-tracking sortie except one, at locations between the Kleinbos and Steilkop (Fig. 14). Recapture occurred six weeks after the last radio contact.

Otter 7, Dougal, was captured on three occasions with an interval of over four months between capture and last recapture. Residential status was confirmed in the course of ten weeks radio-tracking which determined the boundaries of Dougal's home range as the Geelhoutbos to the west and just west of Vermaak se krans in the east (Fig. 14).

As radio-tracking confirmed the residential status of all otters that were recaptured at, or close to, their initial capture site it would seem safe to assume that similar recaptures in any future studies of Aonyx in Tsitsikama will also reliably indicate that the recaptured animal is a permanent resident. Such an assumption is not necessarily valid for inland populations of Aonyx, or possibly even for other coastal populations, as the social organization of the animal may well differ in other habitats. Carnivore social organisation is very flexible, even within a species. Kruuk's (1972) work on the spotted hyaena, Crocuta crocuta, revealed significant differences in social organisation in differing habitats. Differences between marine and freshwater habitats that may lead to variation in the social organization of Aonyx are discussed in the relevant section.

REACTION TO IMMOBILIZATION

The data presented in Table 14 concur with van der Zee's (1979) main conclusion, that *Aonyx* is more sensitive to these drugs than other mustelids and viverrids (e.g. Ramsden *et al.*, 1976; Randall, 1976). A dosage of approximately 10 mg/kg of ketamine and 1 mg/kg of acetopromazine serves as a suitable initial dose. During the present study initial dosage varied between 7,1 - 14,0 mg/kg of ketamine and 0,7-1,2 mg/kg of acetopromazine. Subsequent boosters were injected as required. The highest total dose of ketamine necessary to subdue an otter before handling was 19,6 mg/kg administered to male 8, the smallest otter handled, in conjunction with 1,2 mg/kg of acetopromazine. The highest total dose of acetopromazine necessary to subdue an otter before handling was 1,5 mg/kg for male 1, in conjunction with 16,1 mg/kg of ketamine.

Ataxia in some animals occurred 3½ minutes after the initial dose whereas in others it was delayed until 20 minutes after the initial dose and was only achieved after a booster. Recovery time also showed a wide variation, the most rapid being less than four hours and the longest being over ten hours. The 24 hour recovery time of otter 2 on 26/5/1981 is not included as this animal had undergone surgery and had therefore received a very large booster of ketamine.

No problems were ever encountered in the use of the two drugs and they may be regarded as suitable for the handling of *Aonyx*.

DISCUSSION AND CONCLUSIONS

POPULATION ESTIMATE

The results of the ^{65}Zn technique for estimating populations, shown in Table 17 and Fig. 9 , provide almost equal estimates of population density of *Aonyx* for two separate stretches of coast within the Tsitsikama National Park. The estimate for the section between the Elandsbos River and Rietmondjie (hereafter referred to as the western section) is one otter per 2,0 km of coast compared to one otter per 1,85 km coast for the section between the Elands and Eerste rivers (hereafter referred to as the eastern section). The location of these two stretches of coast, in relation to each other and the Park boundaries can be assessed by reference to Fig. 6 . The eastern section of coast extends approximately 4,6 kilometres beyond the boundaries of the Park. This is an area of increased human activity with two small holiday villages located at the base of the escarpment.

The best assessment of the reliability of these estimates can be made by reference to Kruuk, Gorman & Parish (1980), the paper in which this technique was first described. Kruuk *et al*. (1980) showed that this method gave a reliable estimate of population size for an enclosed group of European badgers, *Meles meles*. With two labelled animals a sample of eighty or more labelled and unlabelled faeces provided a good estimate of group size. This sample size was exceeded for both study areas in the Tsitsikama (446 spraints were collected on the western section of coast and 517 on the eastern section).

The present study would appear to be the first application of this technique to an aquatic mammal, though Jenkins (1980) has used ^{65}Zn to trace the movements of a European otter, *Lutra lutra*, in Northern Scotland.

Though there are likely to be considerable physiological differences between a marine mustelid and a terrestrial mustelid, for example in metabolic rate (Morrison, Rosenmann & Estes, 1974) and electrolyte flux (Costa, 1982), it is not clear how these quantitative differences could affect the reliability of this technique.

The only available methods of corroboration for this estimate are by comparing the two estimates obtained for the separate sections of coast and comparison of these estimates with the estimate made by van der Zee (1979, 1982) and a minimum estimate obtained in the course of the trapping programme conducted during the present study.

The close agreement of the two estimates obtained provides some corroboration in view of the uniform habitat and levels of protection afforded Aonyx within the National Park. The two sections of coast are only separated by 19 km (straight-line distance) and both lie at the base of the steep Tsitsikama escarpment. Thus it seems unlikely that there are significant differences in prey populations and there are certainly no major differences in terrestrial resources (e.g. availability of fresh-water and dense bush for cover). The density of spraints and holts located in the course of the coastal survey (Table 6), does not suggest any difference in the level of the utilisation of these two stretches of coast. The spraint density in the western and eastern sections is 48,2 spraints/km and 51,6 spraints/km respectively while the density of holts is 2,04 holts/km in the western section and 2,45 holts/km in the eastern section. The spraint densities in themselves should provide some indication of the relative population densities of otters in the two sections. Erlinge (1972) assessed the habitat selection of European otter, Lutra lutra, and mink, Mustela vison, on the basis of the occurrence of faeces of the two species.

Erlinge took the number of excrements per sampling area as a rough measure of the density of each species.

Van der Zee (1979, 1981) obtained an estimate of the numbers of Aonyx in the Tsitsikama Coastal National Park, based on the number of holts, the utilisation of those holts, the movements of two females with cubs and an assumed sex ratio of 1:1. The estimate of 33 otters in the whole Park incorporated a number of assumptions and was based on limited data, yet the careful reasoning involved lent some validity to the estimate. This population size would give a density of approximately one otter to every 1,8 km of coast, which is very close to densities estimated by the ^{65}Zn technique (one otter per 1,9 - 2,0 km).

The fact that Aonyx has been protected in the Tsitsikama since 1964, and prior to that suffered little human disturbance due to the isolation and rugged nature of the coast, leads one to expect a relatively stable population size. The close agreement of the two estimates, made only four years apart, is therefore to be expected.

Nevertheless it is somewhat surprising that there is such a close agreement in view of the fact that van der Zee appears to have seriously underestimated the holt density on the coast. Radio-tracking experience in the present study indicated a much higher density of holts within the study area than was initially indicated by a survey of otter sign. It became apparent that some regularly used holts are characterised by a bare minimum of detectable otter sign. This factor alone could serve to explain the discrepancy between van der Zee's (1979) estimate of 51-65 holts in the Park and the estimate obtained during the present study of 120 holts. In one section of coast on which van der Zee located 12 holts, radio-tracking indicated that there was a minimum of 19 holts.

If population size is indeed more or less stable, such a large increase in the density of utilised holts is more likely to be an indication of improved censussing techniques than a real increase in the number of utilised holts.

Taking into account the paucity of data, some of it apparently inaccurate, and assumptions that had to be made, van der Zee's estimate cannot be taken as reliable confirmation of the ^{65}Zn estimate.

Results from the trapping programme conducted during the present study offer the only other potential source of corroboration. Between the Geelhoutbos River, trap-site 5 (Fig. 6), and trap-site 8 which lies east of Stormsriver, a total of ten otters were trapped. This stretch of coast is 15,3 km long so at first inspection the otter density appears to be 0,65 otters per km or one otter per 1,53 km. However for reasons that are elaborated in the discussion on social organization it seems likely that five of these otters, four caught at trap-site 5 and one caught at trap-site 8, are restricted to ranges west of Skilderkrans or east of Steilkop. This leaves a minimum of five otters, four males and one female, as the apparent exclusive residents of the coast between Skilderkrans and Steilkop, a straight-line distance of 9,0 km. Only four of these animals, all the males, were certainly resident, but the female trapped at holt 5 (trap-site 4) in the centre of this 9 km stretch was probably resident. A minimum estimate of otter density on this section of coast is therefore 0,44-0,55 otters per km or one otter per 1,8 - 2,25 km. This estimate is in close agreement with the ^{65}Zn estimate but, as was the case with van der Zee's (1979) estimate, is based on a number of assumptions (see discussion on social organization).

In the absence of any other estimates a mean of the two estimates of otter density obtained from the ^{65}Zn technique is taken as a reliable indicator of the density of Aonyx in the Tsitsikama. This mean is 0,52 otters per km of coast or approximately one otter per 1,9 km, that is 30-31 otters in the whole Park. Apart from van der Zee's estimate, the only estimate of population density in Aonyx is from Tayler (1970) who reported seven adults on a 35 km stretch of coast near Port Elizabeth. No estimates of population density of Aonyx in freshwater systems have been published.

Aonyx in the Tsitsikama was rarely observed fishing further than 100 m from the shore, and usually less than 50 m. The width of the intertidal and subtidal zones exploited by Aonyx may therefore be taken as 100 m. A 1,9 km length of coast is thus equivalent to 0,19 km^2 or 19 ha of water surface. Using this estimate it is possible to compare the population density of Aonyx with the published estimates for two other lutrines. These estimates for Lutra lutra, the European otter (in freshwater and marine habitats) and Enhydra lutris, the sea otter, are shown in Table 33 , with the estimate from the present study for Aonyx.

TABLE 33

Estimates of population density for three lutrines.

Species	Habitat	Geographic location	Density - water surface per otter (ha)	Author
Lutra lutra	Freshwater	Southern Sweden	70 - 100	Erlinge (196
Lutra lutra	Marine	Shetlands, Scotland	± 17	Watson (1978
Enhydra lutris	Marine	Amchitka, Aleutian Islands	3,3 - 5	Estes & Palm sano (1978)
Enhydra lutris	Marine	Monterey, California	± 6	Loughlin (19
Aonyx capensis	Marine	Tsitsikama, South Africa	± 19	Present stud

There is wide variation in ecological factors between the different habitats listed in Table 33 . This variation combined with morphological and any physiological differences between the otter species has yet to be studied so any attempt to explain the variation in otter densities is speculative. Given the lack of information only tentative explanations can be offered for even the widest variation in population densities.

Watson (1978) suggested that the sea-coasts inhabited by *Lutra lutra* in the Shetlands are the optimum habitat for otters. This explanation for the much higher otter density in the Shetlands than in the freshwater system in southern Sweden (Erlinge, 1968) was rather vague as Watson made no attempt to define the term optimum. As food is often the most critical resource for an animal (Wynne-Edwards, 1962) it may be that prey densities for *Lutra* are much higher on the coast. There are however no figures relating to prey densities.

Similar variation may exist between freshwater and marine populations of *Aonyx* but as yet there are no estimates for density in inland populations of this species.

The very high population densities seen in *Enhydra* may also be linked to food resources. The kelp beds which they inhabit have a very high net primary production (Mann, 1973). Estes & Palmisano (1974, 1978) have shown that very high prey densities are maintained in these kelp beds, even when subject to intense otter predation. This factor alone may account for much of the discrepancy between densities of *Enhydra* and those of marine populations of *Aonyx* and *Lutra*.

RADIO-TRACKING - DISCUSSION AND CONCLUSIONS

ACTIVITY PATTERNS

Reference to Figure 11 and Table 18 indicates that Aonyx in the Tsitsikama Coastal National Park is predominantly nocturnal. In the three otters radio-tracked during three different seasons, the peak of activity invariably occurred at night, between 20h00 and 22h00. The mean percentage activity was significantly higher at night than during the day in all three otters. Mean percentage activity at sunrise and sunset was also higher than during the day, and generally higher at sunset than sunrise (Table 18).

The fact that the three otters were radio-tracked in spring (Biggles), summer (Fat Freddy) and winter (Dougal) makes some examination of seasonal variation in activity pattern possible. However, it is not possible to draw firm conclusions from the results since different otters were radio-tracked at different times of the year. Individual and seasonal differenc in behaviour cannot therefore be distinguished. As little was known about individual differences that might lead to variation in activity pattern, the only hypotheses suggested to account for this variation are based on seasonal differences.

The results show that Dougal, tracked during the winter, has a significantly higher level of diurnal activity than either of the other two animals. Though his level of diurnal activity was still low, Dougal was observed foraging between 10h00 and 16h00 on thirteen occasions. This was never recorded for Biggles (tracked in spring) or Fat Freddy (tracked in summer). Furthermore it is clear that Dougal was far less active than the other two animals between 23h00 and 06h00. This behaviour is reflected in differences in the ratios of nocturnal : diurnal activity presented in Table 18. The ratio for Fat Freddy is nearly three times higher than that for Dougal.

If this variation is due to seasonal changes in environmental conditions, a likely explanation would appear to be variation in mean sea temperature. Water temperature is more likely to limit foraging activity in aquatic mammals than air temperature is in terrestrial mammals as thermal conductance is higher in water than air. Morrison, Rosenmann & Estes (1974) found that thermal conductance in the sea otter, _Enhydra lutris_, was twice as high in water as in air.

As mean sea temperatures are lower in winter than they are in summer the problem of heat loss will be greater for _Aonyx_ in the winter months. This could result in _Aonyx_ minimising the proportion of time it spends in the water during the winter. The lower overall percentage activity of Dougal (tracked in Winter) as compared to Biggles and Fat Freddy (tracked in spring and summer respectively), could therefore be a response to this fall in mean sea temperatures.

A possible explanation of the predominantly nocturnal activity pattern and peak of activity between 20h00 and 22h00 is that prey availability increases at night. _Plagusia chabrus_, the red rock crab, one of the otter's main prey items, forages actively at night, leaving the crevices it occupies during the day (_pers. obs._). This will render the crab more vulnerable to predation. Curio (1976) notes that some predators are known to synchronize their predatory activity with the main activity of their prey.

Some of the fish species preyed upon by _Aonyx_ may also be more vulnerable at night since some fish species can be approached more easily at night (Allen _pers. comm._).

Smithers (pers. comm.) reports that Aonyx is more active during daylight hours in freshwater in parts of Botswana and Zimbabwe than is the case in Tsitsikama. Though the animal should still be regarded as crepuscular it is often seen actively foraging in mid-morning and mid-afternoon. However Aonyx still apparently ceases foraging in the middle of the day in these freshwater habitats. Any such differences in the activity pattern between Aonyx populations in freshwater and those on the coast may be related to the different prey species taken in the two habitats.

The only other lutrine for which comparable data exists is the sea otter Enhydra lutris. Shimek & Monk (1977), working on Enhydra at Monterey in California recorded peaks of foraging activity at 07h00, 17h00 and probably 24h00. The peak at 17h00 was longer than that at 07h00. Loughlin (1980), working in the same area, showed that there was considerable individual variation in the timing of activity peaks. Some animals displayed a tendency for nocturnal foraging, others for diurnal foraging and yet others showed no preference. No explanations were offered in either study for the observed patterns of activity.

The daily pattern of foraging illustrated in Figure 12 , is not uncommon among mammals, especially rodents and insectivores (Curio, 1976). Some other carnivore species have been found to be active in bursts, notably the sea otter, Enhydra lutris (Loughlin, 1980). As this pattern of foraging is by no means specific to Aonyx and Enhydra it is not an adaptation to a marine environment. Aonyx may be limited to foraging in bouts due to the higher thermal conductance of skin and pelt in water as opposed to air. This would require a threshold, presumably measurable in terms of body temperatures that determines the length of a foraging bout.

An animal is forced to leave the water when body temperature falls below this threshold, to prevent further decline. Body temperature would increase again while resting ashore due to the lower thermal conductance of air. However the wide variation in the duration of foraging bursts (mean duration = 70,0 ± 46,1, (S.D.), range = 10 - 225 mins, n = 75) at all sea temperatures suggest that this hypothesis is an oversimplification. This explanation could also apply to _Enhydra_ in California even though this otter does not come ashore to rest, merely floating on its back in the kelp beds during periods of inactivity (Loughlin, 1980). Shimek & Monk (1977) pointed out that when the animal floats on its back, the areas where the fur is thinnest (face, forepaws, flippers and tail) are held out of the water. This will reduce heat loss in water and may also increase _Enhydra_'s ability to absorb radiant energy from the sun (Shimek & Monk, 1977).

Foraging bouts generally lasted longer in _Enhydra_, the shortest measured being longer than an hour, compared with ten minutes for _Aonyx_. Overall, _Enhydra_ spent 34% of its time budget engaged in active foraging as compared with 18-25% for _Aonyx_. This may be a reflection of higher energy requirements due to _Enhydra_'s habit of remaining at sea during rest periods.

An alternative hypothesis is that timing and duration of foraging bouts is largely determined by hunger and satiation. Factors other than satiation (e.g. reduced body temperature, behaviour of conspecifics, hunting success) may also affect the termination of foraging. The foraging behaviour of an animal such as _Aonyx_ is affected by a variety of factors and oversimplification is always a danger when trying to explain the pattern of this activity.

RANGE SIZE

Examination of Figure 13 indicates that in the case of Dougal the fifty-fourth radio fix resulted in a 3,5 km increase in the estimate of range size. As no other radio-tracked otter was located on more than 25 separate occasions the range estimates for these animals are almost certainly incomplete. The increase in radio-tracking success with time (Table 19) is also likely to have contributed to the progressive increase in the estimated size of ranges. These factors necessitated some extrapolation of the results based on the range estimate of Dougal and what is known of the social organization of Aonyx in Tsitsikama.

Examination of the ranges at least partially mapped for six males (Fig. 14) suggests that these six animals can be divided into two groups on the basis of the overlap of these ranges. Eric, Fat Freddy, Dougal and Oleg form one group, Biggles and Naffer (died during radio-tracking) the other. In the Discussion on social organization (see later) it is suggested that these groups are clans, as defined by Kruuk (1978a). As such the members of each group would be expected to have similar limits to their ranges. So if Eric, Fat Freddy and Oleg had been tracked over longer periods, their range limits would presumably have approached those of Dougal. The same applies to Naffer and Biggles.

The proof for this type of social organization, details of the clan members' relationship to one another and possible relationships with members of other clans, is presented elsewhere. The relevant point here is that the range estimate for Dougal is likely to be a better estimate of the range sizes of Eric, Fat Freddy and Oleg than those shown in Figure 14 . The estimates given for Eric and Fat Freddy are by no means useless as they probably serve to indicate the most heavily utilised portion of the clan range (see later). After two and a half months of radio-tracking one may assume that the extreme limits of Dougal's range had been fixed. Radio-tracking indicated that Dougal rarely visited these extreme limits (see below).

The extent of overlap of ranges of neighbouring clans is not clear as Biggles was only tracked for two weeks. It is therefore unlikely that the extreme limits of his range are known. The known western limit of his range coincides with the eastern limit of Dougal's range so there is certainly some overlap. This is discussed further in the section on social organisation.

The size of ranges, expressed in terms of linear extent, is shown in Figure 14. To facilitate comparison with other otter species it is necessary to convert minimum range sizes into home range estimates.

For the purposes of the following Discussion home range is defined as the area travelled by an individual in carrying out its routine activities (Jewell, 1966).

The home range estimate for Aonyx was based entirely on the range size of Dougal as he was the most comprehensively tracked otter. His home range was taken as including all those areas visited at least twice in the course of radio-tracking. On this basis his home range extended from holt 33, just east of the Kleinbos River to holt 38, at the Langbos River, a straight-line distance of 15,0 km (Fig. 14).

Aonyx was rarely seen fishing more than 100 m from the shore and was usually closer. The maximum width of the littoral and sub-littoral zones utilised may therefore be taken as approximately 100 m wide. Thus in the case of Dougal a home range with a linear extent of 15,0 km, comprises approximately 150 ha of water surface. The linear extent in km of all the otters' known ranges, shown in Fig. 14 , can be converted into area measured in hectares by multiplying by a factor of ten.

A minimum range size estimate for one female of 14,3 km of coast was obtained as a result of application of the radio-active labelling technique (see Population Estimate Results, Discussion and Conclusions). Observations indicate that Aonyx restricts foraging activities to within 100 m of the coast (see above) so minimum range area is approximately 143 ha.

Comparison with other otter species in coastal habitats reveals that Aonyx has largest known ranges in terms of the length of coast used but not in terms of area of sea surface. Estimates of length and sea surface area of home ranges of other lutrines in marine populations are compared in Table 34 with the estimates obtained for Aonyx in the present study.

TABLE 34

Estimates of home range size in coastal otter populations

Species	Sex	Home range length of coast (km)	Home range area of sea surface (ha)	Author
Lutra lutra	Male	>3,2	-	Watson (1978)
Lutra lutra	Female	2,5	35	Watson (1978)
Enhydra lutris	Male	-	75-125	Calkins & Lent (1975)
Enhydra lutris	Male	-	41	Loughlin (1980)
Enhydra lutris	Female	-	80	Loughlin (1980)
Enhydra lutris	Male	1,0-2,7	80-460	Ribic (1982)
Enhydra lutris	Female	4,3-6,4	470-680	Ribic (1982)
Aonyx capensis	Male	15,0	150	Present study
Aonyx capensis	Female	14,3[x]	143[x]	Present study

[x] These figures refer to minimum range size and not home range size

Note that female home range sizes are consistently higher than male home range sizes in *Enhydra*. This does not appear to be the case in *Lutra lutra* and also seems unlikely in *Aonyx* as the area of peak utilisation (core area) of males is probably larger than that of females (see Discussion on home range utilisation).

A possible explanation for the narrow home range of *Aonyx* is the steeply shelving seabed in Tsitsikama. Ribic (1982) showed that *Enhydra* home ranges were much wider at San Simeon than Monterey (Loughlin, 1980) where the seabed shelves more steeply and the kelp zone is consequently narrower.

RANGE UTILISATION

The detailed break down of spatial variation in the levels of range utilisation is illustrated in Figures 19, 20 and 21.

There was a bias in the results of total foraging time per section due to the position of the rest camp in the centre of Dougal's range. As a radio-tracking search invariably started at the rest camp if the animal was in this central section it was located earlier and therefore tracked for longer than if it was initially located at either end of the range. Therefore, there is some overestimation of the utilisation of the central section of Dougal's range.

This bias did not affect the data collected for Fat Freddy to such an extent as the animal was tracked intensively over a shorter stretch of coast. There was no bias at all in the data collected for Biggles as there was no consistently used starting point for the initial search.

The data collected on the two otters tracked to the west of the Geelhoutbos River, Naffer and Biggles, were limited by the short duration of the tracking periods. Naffer was tracked for five days out of six immediately after release and was then lost until his body was recovered sixteen days later. During this short period Naffer spent the majority of his time in sections 21-23 (Fig. 19). Similar intense utilisation of limited stretches of coast for short periods was recorded for other otters. Naffer was not located during a search between the Lottering and Geelhoutbos rivers on one of the first six days before radio contact was lost completely. Therefore his range is undoubtedly more extensive than indicated in Figure 14 .

Biggles was tracked over a period of fifteen days during which the animal used at least 13,3 km of coast. The sample sizes for individual sections are too small to draw meaningful conclusions on spatial variation in the levels of utilisation. There is some indication that sections 4-11 and section 21 may be favoured foraging areas (Fig. 19). It is worthy of note that section 21 is in the section heavily utilised by Naffer.

The record of total foraging time spent in each section indicated that section 11, at the mouth of the Witels River was heavily utilised. However most of the data for section 11 were collected in the course of a single night of foraging and therefore may not be truly representative.

Eric was not only the first otter to be tracked either side of Stormsriver, but also the first otter tracked in the study. The data collected in the course of this tracking were rather fragmentary (Table 19). On two days the whole of the animal's known range was searched without success. Eric's range must therefore extend further than the limits depicted in Figure 14 . The significantly higher level of utilisation of sections 49-53 may be an overestimate.

Fat Freddy was initially tracked intensively over a period of fourteen days, then less intensively for a further three weeks. On one day the whole of the known range was covered without locating the animal. The full extent of Fat Freddy's range is therefore not known.

Statistical analysis of the frequency of fixes per section (Fig. 20) indicates that sections 43-45 are subject to significantly higher levels of utilisation than the remaining sections (Table 21).

Dougal was the last otter to be radio-tracked, intensive tracking being conducted for 44 days and tracking at irregular intervals conducted for a further 29 days. The 19,5 km extent of the range made adequate coverage of the limits of the animal's range difficult. There is therefore likely to be some overestimate of utilisation towards the centre of the range. However the animal was located during 44 out of 47 searches, so any such bias was minimized by improved radio-tracking techniques.

A striking feature of the frequency distributions of fixes is that the 17 most heavily utilised sections of Dougal's range coincide closely with the known ranges of Fat Freddy and Eric. The fact that both Fat Freddy and Eric were located more often inside their range than missed altogether (Table 19) suggests that the majority of their activities were confined to the known limits of their range. These three animals therefore share the same area of most intense utilisation. This section of the clan range is hereafter known as the core area, a term first used by Kaufmann (1962) to describe the most intensively used zone of the home ranges of coatis, Nasua narica. Kaufmann (1962) noted that the core areas amounted to territories, a designation suggested for the core areas of Aonyx in Tsitsikama (see Discussion on Territoriality).

Within this core area there are recognizable peaks of utilisation, which in the case of Eric and Dougal coincide (sections 49-53 and 49-54 respectively). Peak utilisation for Fat Freddy is seen in sections 43-45 and it is interesting to note that there are small peaks in section 43 for both Dougal and Eric. Examination of the utilisation in terms of foraging time per section (Fig. 21) indicates intensive foraging by Fat Freddy in section 44 and by Dougal in sections 49 and 53. Intensive foraging in a limited area suggests a locally abundant food resource. The peaks in home range utilisation may therefore be a response to local variations in prey availability.

There is no evidence for peaks of utilisation in the sections at either end of Dougal's range or even at either end of the shared core area. If the otters were engaged in active defence of their range peaks of utilisation would be expected at range boundaries. This is not to say that there is no defence, only that territoriality is not mediated by frequent physical encounters at territorial boundaries. The implications of this are discussed in the section on social organization.

The method used for estimating the population density of Aonyx, intramuscular injection of ^{65}Zn, provided information on range utilisation in females (see Population Estimate Results and Fig. 9). Eight-two per cent of the radio-active spraints found within the range of the labelled female released near Gammelbaai (Fig. 9) were found in the central 5,7 km of the animal's known range. This compares with 85% of the radio fixes of Dougal confined to an 8,5 km central section of his range. No firm conclusions can be based on data collected from only one animal of each sex.

It is not clear if core areas or even range boundaries of males and females coincide. There is some evidence to suggest that females will not trespass in the males' core area of a neighbouring clan (see Population Estimate Results and Fig. 9).

The only coastal population of otters for which similar home range utilisation data exist, is the population studied by Watson (1978) in the Shetlands. A female and cub using 2,5 km of coast displayed peaks in foraging activity in the centre of the range and at one end of it. There was no clearly defined central core area but the two areas of peak activity may constitute separate core areas.

Enhydra lutris appears to have separate foraging and resting areas (Shimek & Monk, 1977; Loughlin, 1980; Ribic, 1982) and hence no single identifiable core area. However as particular areas are favoured for particular activities, areas of intense utilisation may be recognised if each activity is considered separately. The existence of separate areas of intense utilisation for different activities will have a major influence on the movement patterns of the animal (see below).

MOVEMENT PATTERNS

The present study yielded a considerable amount of data on the movement patterns of Aonyx within their ranges. In the absence of detailed information on the littoral and sub-littoral foraging areas of Aonyx it was not possible to relate these movements to ecological factors. The recorded movements could therefore only be examined for recognisable patterns.

The movement patterns of otters in the course of a single night track were sometimes very localized (Fig. 15 b & c, 16 b). On other occasions the animals would cover large sections of the coast in one night (Fig. 16 a, c and d).

The function of these two patterns of movement can only be speculated upon given the available information. Repeated course reversals may be analagous to the area restricted searching seen in many insect predators and parasitoids (Krebs, 1978) and some birds (e.g. Smith, 1974b). This type of searching appears to be a response to clumped prey distributions (Waage, 1977 and Smith, 1974b). Personal observations made in the course of hunting Plagusia chabrus and Octopus granulatus in the littoral zone suggested that populations of Plagusia show some clumping.

Long distance movements during foraging may be the norm when clumped prey is not located. Alternatively this behaviour pattern may have a social function. On some nights (e.g. Fig. 16 c) when an animal covered a long stretch of coast, short visits made to some holts were not for the purposes of resting. The animal may have deposited a spraint or an anal gland secretion in the course of these visits. As such visits were only recorded during the night observation of the animal's behaviour was not possible. However, Lutra lutra, in a freshwater habitat, is known to move long distances purely for the purpose of depositing spraints at established spraint sites (Erlinge, 1968). This does not prove that Aonyx behaves in a similar fashion.

Movements of otters taking place over a period of days rather than a period of hours are plotted in Figures 15 a and 17 a - d. With the exception of the track of Biggles, illustrated in Fig. 15 a, the movements of the otters appear erratic. Successive daily fixes were separated by as little as 250 m straight-line distance (S.L.D.) or as much as 7,3 km. Abrupt reversals of course were common.

The only obvious pattern to emerge from the plots of Eric, Fat Freddy and Dougal is the restriction of the animal's movements to a common core area. This core area, previously identified in the Discussion of range utilisation, extended from holt 9 to just east of holt 7, sections 37-53 (Fig. 18). Abrupt reversals of course can be seen at the boundaries of this core area in Figs 17 a, b and c. The three movements recorded outside this core area in Figs 17 b, c and d are of limited duration, the animals being located outside the core area on only one day on each occasion. It may be that the stretches of coast immediately outside the core areas are zones of overlap between neighbouring clans.

The track of Biggles recorded in Fig. 15 a is in complete contrast to those recorded for Eric, Fat Freddy and Dougal. The radio fixes taken on six successive days reveal a steady progression along the coast from east to west, in the course of which Biggles travels 11,8 km (S.L.D.). Unfortunately this animal was not tracked for long enough to establish the limits of his core area, if indeed he had one.

A possible explanation for Biggles' steady progress along the coast is that he was released on the day the illustrated track commences.

As he had been held in captivity for six days prior to this movement, it may simply have been an artefact of his release. Alternatively he may have been re-establishing his presence by covering his entire home range.

Little is known of the foraging patterns or day to day movements of other otter species, the data that have been collected largely referring to isolated observations. Kruuk & Hewson (1978) noted that L. lutra on the Ardnish peninsula swims up to 700 m to foraging areas where they then spend up to two hours foraging in a restricted area. On completion of foraging otters were often seen to return to the original holt. Watson (1978), working on L. lutra in the Shetlands mentioned only that foraging otters worked gradually along the coast. L. lutra in the Shetlands therefore displays a similar foraging technique to Aonyx capensis. Watson (1978) gave no indication of the frequency with which Lutra returned to the original holt.

Shimek & Monk (1977), Loughlin (1980) and Ribic (1982) all noted long distance movements to foraging areas in sea otters, Enhydra lutris. After foraging in a restricted area the animals returned to their original resting place, usually social groups of Enhydra floating in the kelp beds. Movement patterns therefore resemble those of the L. lutra population studied by Kruuk & Hewson (1978) more closely than those of Aonyx capensis on the Tsitsikama coast and L. lutra in the Shetlands (Watson, 1978). A possible explanation for this fundamental difference is that the prey distribution of E. lutris in California and L. lutra on the Ardnish peninsula is more clumped than that of L. lutra in the Shetlands and A. capensis in Tsitsikama.

HOLT UTILISATION

The overall utilisation of individual holts by a number of otters was measured indirectly by recording the occurrence of otter sign at those holts (see Coastal Survey - Results and Discussion). Radio-tracking made it possible to measure the frequency of utilisation of different holts by the same otter.

Of the holts used by any one otter, some are used far more frequently than others (Table 22). The holt utilisation ratio, calculated for only three of the otters indicates that some holts are frequently passed without a visit whereas others are never passed without being occupied.

Only for Fat Freddy and Dougal are there sufficient data to make an assessment of variation in holt utilisation. Fat Freddy utilised holt 4 most frequently and Dougal showed a distinct preference for holts 1 and 7. The location of these favoured holts coincides with the area of peak foraging activity of each animal. Foraging activity is recorded in Fig. 21 , the location of holts in relation to the numbered sections of coast is shown in Figure 18 . Frequency of utilisation of a particular holt and total observed foraging time in the adjacent section of coast shows significant positive correlation for both Dougal and Fat Freddy (see Results). These results indicate that the utilisation level of holts is to some extent determined by the location of the preferred hunting areas.

There was no significant correlation between the levels of utilisation recorded during radio-tracking and the levels recorded by variation in numbers of spraints found at holts (see coastal survey). A possible explanation for this is that the utilisation data for only two clan numbers was used in the assessment. If all or at least most of the otters inhabiting the area between George se baai and Steilkop had been radio-tracked, correlation of the two measures might well have been significant.

Variation in the utilisation of holts is apparently not restricted to the frequency of occupation. Occupancy of some of the holts used by Dougal was only recorded at night (holts 2, 10, 13 and 34). It may be that such holts are only used for the shorter rest periods between forays at night. However a test of the duration of Dougal's completed rests in different holts indicated that there was no consistent significant difference (see Results).

A minimum of three adult males, all members of the same clan, were known to be using the same holts during the same period. This raises the question of whether utilisation of holts by individual clan members bears any relationship to utilisation by other clan members. There was no significant correlation between Fat Freddy's and Dougal's utilisation rates of different holts. There was however a tendency for Fat Freddy to avoid the holts most heavily utilised by Dougal and vice versa (see Results). Simultaneous radio-tracking of at least two otters is required to investigate the influence of other clan members on one animal's pattern of holt utilisation.

There is very little information on the patterns of holt utilisation in other lutrines. Kruuk & Hewson (1978), working on L. lutra on the Scottish coast obtained evidence to suggest that individual otters were restricted to one main holt. There was however no conclusive proof. Watson (1978) working on L. lutra in the Shetlands found that though holts were sometimes occupied by two adult females simultaneously, each female had a main holt which she sometimes actively defended against intruders.

The available information suggests that both these populations of _L. lutra_ have a social organization that bears little resemblance to that of _Aonyx_ in the Tsitsikama. Kruuk (pers. comm.) now working on _L. lutra_ in the Shetlands has preliminary evidence to suggest that social groups consist of family groups based on one adult pair. Differences in social organization and in habitat variables such as prey distribution will affect the patterns of holt utilisation displayed by an otter population.

FORAGING BEHAVIOUR

The tests of correlation between foray variables investigate the physical limitations of Aonyx. For example, a significant positive correlation between the duration of a foray and the duration of the subsequent rest would suggest that the otter's stamina is limited so that he requires a longer rest after a longer foray. It is important to stress that correlations do not imply cause and effect.

The positive correlation between mean foray speed and foray displacement in both Dougal and Fat Freddy indicates that the further an otter travels in the course of a foray, the greater is his speed through the water. This implies either that the otter is foraging less intensively or that he is adopting a different foraging strategy during long-distance forays. Observations made during diurnal forays suggest that the former hypothesis provides the explanation. Animals making long distance forays were sometimes observed up to one hundred metres from the shore swimming steadily and making very few, if any, foraging dives. This contrasted with intensive foraging seen during forays of shorter displacement during which an animal would remain within 50 m of the shore, progressing slowly with frequent foraging dives. Foraging in a restricted area for periods of 10-15 minutes was a characteristic feature of this intensive foraging. Some forays recorded showed a combination of the two behaviour patterns, the animal initially displaying intensive bouts of foraging dives, then moving further offshore and swimming steadily with fewer foraging dives. Forays of greater displacement sometimes terminated with a short bout of intensive foraging.

Thus it appeared that though the otters invariably foraged intensively at some stage in the course of the foray, some forays had the additional function of long-distance movement. The purpose of the long-distance movement can only be speculated upon. It may be a response to a local depletion of prey populations, the animal moving to alternative hunting areas. Alternatively the movement may have a social function. The animal may travel long distances to visit and mark a particular holt, a behaviour pattern seen in Lutra lutra (Erlinge, 1968) (see Social Organisation - Discussion).

The positive correlation between foray duration and foray displacement in both Dougal and Fat Freddy indicates that despite the higher mean speed forays of greater displacement usually take longer to complete than forays of shorter displacement, a result that is not unexpected. Furthermore, if prey capture rate is indeed lower during forays of greater displacement (see Observations on predatory behaviour), foraging bouts of longer duration would be required to compensate for this.

The absence of significant negative correlation between foray speed and foray duration or significant positive correlation between foray duration and subsequent rest time suggests that physical exhaustion is not an important limiting factor during foraging.

The only environmental factors that affect the four foray variables appear to be sea temperature, tide state and time of day.

None of the four foray variables of Dougal showed any significant correlation with sea conditions.

Foray duration, foray displacement and the duration of the subsequent rest showed no correlation with sea temperature. However the mean foray speed of Fat Freddy showed a significant negative correlation with sea temperature and that of Dougal a significant positive correlation.

In view of this dramatic shift in correlation from negative to positive it seems unlikely that the relationship between sea temperature and mean foray speed is simple.

As different individuals were tracked in different seasons it is not possible to differentiate between individual variation and seasonal variation as explanations for this reversal of the response to sea temperature. Seasonal variation seems more plausible in view of the seasonal change in mean sea temperatures (Fig. 4). However individual variation cannot be ruled out. For example, a possible explanation for the observed correlations is that the two animals radio-tracked specialise in prey items with different responses to changes in sea temperature.

It is not possible to distinguish between individual and seasonal variation in preferences for particular tide states. A plausible hypothesis to explain the preference of Biggles and Fat Freddy for low tide is exposure of the littoral zone and shallower water in the sub-littoral zone during this tide state. This would presumably facilitate prey capture. There is no obvious explanation for Dougal's preference of high tide.

Only Fat Freddy showed significant variation in nocturnal and diurnal foraging behaviour. A possible explanation for the slower mean foray speed during the day is that the animal foraged less intensively at night. However there was no significant increase in foray displacement at night as might have been expected. Rest times were significantly shorter during the day, but sample size is too small to provide a basis for conclusions.

The positive correlation between the mean foraging speeds of Fat Freddy and Dougal is 90% significant but does not attain the 95% level of significance. As the sample size is small the 90% level of significance does not provide a sufficient basis for conclusions.

The significant negative correlation between the measure of Dougal's home range utilisation and mean foraging speed suggests that the most heavily utilised sections are subject to the most intensive foraging. This conclusion rests on the assumption that slower mean foraging speed is a reliable indicator of more intensive foraging. This correlation does not hold for Fat Freddy but it is not clear what the implications of this result are. Sample size was smaller for Fat Freddy (n=9) than for Dougal (n=17) - more data might have resulted in a significant correlation for Fat Freddy.

The only comparable data on the foraging behaviour of otters in a marine environment were collected by Watson (1978) studying *Lutra lutra* in the Shetlands. Unfortunately as his observations were made without the benefit of radio-tracking they are rather fragmentary. Nevertheless it appeared that this species also showed preferences for foraging during particular tide states and furthermore, that there was seasonal and individual variation in these preferences.

To fully assess the effect of environmental conditions on the foraging activity of *Aonyx* it would be necessary to quantify the profitability of foraging bouts and not just variables such as foray duration and foray displacement. The tests recorded above only indicate factors which affect some parameters of the foraging activity of *Aonyx*, and not how these factors affect the fitness of *Aonyx*.

PREDATORY BEHAVIOUR

To investigate the possibility of a selective advantage accruing to cooperative hunters, foraging success rates were checked for significant variation between solitary and group foragers. Such variation could take the form of variation in the ratio of successful : unsuccessful dives or in the proportions of prey species caught (some prey species are calorifically more rewarding than others, see page 55). There is no significant variation between solitary and group foragers in either of these measures of success rates. However, the sample sizes are not large so no firm conclusions should be based on these results.

Even if these results are a true reflection of the situation they do not rule out the possibility that cooperative hunting increased foraging efficiency. For example group foragers may display a shorter mean duration of successful dives than solitary foragers. In this case prey profitability (Krebs, 1978) of group foragers will be higher as less energy is expended in the capture of each prey item. Increased foraging success is not the only selection pressure that could have led to the formation of social groups in *Aonyx* (see Discussion on social organisation).

Kruuk & Hewson (1978) showed that duration of successful and unsuccessful dives of *Lutra lutra*, foraging off the west coast of Scotland, varied significantly. This was not the case with *Aonyx*. However, only 26 dives were timed for *Aonyx* as compared to 120 for *Lutra lutra* (Kruuk & Hewson, 1978). It is interesting to note that unsuccessful dives of *L. lutra* were far more frequent than those of *Aonyx*. Overall success rate of observed dives in *Aonyx* was 61,2% (n = 85) compared to 19,1% (n=120) for *Lutra*, a highly significant difference (χ^2 = 37,84, 1 df, P < 0,001). The combination of these two factors in *L. lutra*, far lower success rate and longer duration of unsuccessful dives, compared to successful dives suggests that this species has to work considerably harder for its living than *Aonyx*. This is likely to be reflected in differences in the social organisation of the two species (see Discussion on social organisation).

The fact that Dougal catches a significantly higher proportion of fish than other otters observed does not prove that *Aonyx* shows significant individual variation in preference for or ability to capture different prey species. Variation may be due to local or seasonal differences in prey availability.

It is interesting to note that Dougal was tracked during the winter. It may be that ectothermic free-swimming prey such as fish are more vulnerable to predation at the lower mean sea temperatures prevalent in the winter (Fig. 4). Ectothermic benthic prey such as crabs, which rely on concealment rather than flight as an anti-predator strategy are unlikely to be similarly affected.

There are no figures for rate of prey capture during bouts of intensive foraging in other otter species with which to compare the rate recorded in *Aonyx*. However, Watson (1978) calculated a mean prey capture rate based on total foraging time of *Lutra lutra* in the Shetlands. The rate varied between 0,023 - 0,059 prey items min.^{-1}, compared to the mean of 1,1 prey items min.^{-1} recorded for *Aonyx* during intensive foraging. As intensive foraging bouts lasted for periods of up to 35 minutes it seems likely that if the rate of prey capture in *Aonyx* could be calculated for total foraging time, it would be much higher than that recorded for *Lutra lutra*.

The prey capture rates make no reference to size or calorific value of the prey items caught. It is therefore not clear in what way *L. lutra* might compensate for a lower prey capture. Adult L. lutra in the Shetlands have an approximate adult mean mass of 6 kg (Kruuk, pers. comm.) and this smaller body size will at least partially compensate. Other factors that may be involved are a greater proportion of total time budget spent on foraging, specialisation in larger prey items and prey items of higher calorific value.

GROUP FORAGING

As all the otters radio-tracked were adult males the seasonal variation in group sizes recorded in Table 30 reflects variation in the social behaviour of males. The recorded group sizes suggest that males tend to be solitary from late spring to late summer, but more social from early autumn to early spring. Some of the foraging groups observed between April and September were known to include at least two adult males.

The timing of the breeding season in midsummer (van der Zee, 1979) may provide the explanation for these results. As male reproductive success is limited in many species by the number of matings a male can achieve (Parker, 1978) there is likely to be competition among males, even of the same clan, to obtain matings. Assuming that this is the case if males remain solitary the occurrence of potentially injurious fights over females will be reduced. If there is a dominance hierarchy among the males which obviates fights over females, the sub-dominant animals will have a greater chance of obtaining a mate if they forage alone. However, groups of males may still form in the presence of females on heat. Whatever the details of the social organization the outcome is likely to be the same - males will tend to be solitary foragers during the breeding season.

The seasonal variation in group size recorded in incidental observations of foraging otters is less clear cut (Table 31). The proportion of solitary foragers in the two periods is similar, the significant variation being due to the much higher proportion of groups of three or more otters between October and March. This variation may be partially accounted for by sightings of family groups during the breeding season.

Family groups will be at their largest immediately after the cubs first swim which appears to be in mid to late summer (van der Zee, 1979). Once breeding is complete family group size can only fall as a result of cub mortality or attainment of independence.

There is no obvious explanation for the higher proportion of pairs recorded during incidental observations between April and September.

The significant variation in group size for October to March between the two sources of results, radio-tracking and incidental observations, is probably due to the fact that only males were radio-tracked (see above). Incidental observations would have included family groups of females and cubs whereas the radio-tracked males were invariably solitary (see above).

All the data collected on the cohesiveness of foraging groups refer to radio-tracked males. These foraging groups often consisted largely or even entirely of adult males. On two occasions foraging pairs were both identified as adult males and on a further two occasions at least two out of three foraging animals were adult males. This is not to say that such foraging groups never include adult females (see Results).

Family groups including a female and her cubs are presumably far more cohesive and would not display the casual formation and dispersal seen in these radio-tracked groups.

Identification of the selective pressures which lead to the formation of foraging groups of adults is a matter for speculation. Improved hunting success of groups compared to solitary animals could not be ruled out as prey capture rate was only compared in crude terms. It was not possible to compare the efficiency (Krebs, 1978) of hunting alone or in groups.

Defence against predators seems an unlikely alternative as the only potential marine predators are sharks (van der Zee, 1979) whose ability to prey upon *Aonyx* is unlikely to be significantly affected by the size of foraging groups.

Resource defence may be a function of group foraging if one assumes that defence of the clan's core area depends to a large extent on aggressive encounters in which residents outnumber intruders (see Discussion on territoriality). As aggressive encounters are rarely observed (see Results) this hypothesis is difficult to test.

The incident in which Dougal and Oleg were seen to share food, caught by the latter, suggests that foraging groups may include individuals that are closely related or display reciprocal altruism (Trivers, 1971). If these clan members are close relatives the behaviour could be explained by kin selection (Hamilton, 1964). The existence of such relatedness between members of a social group has been proven in a number of carnivore species (Mech 1970, Kruuk 1972, Schaller 1972, Rood 1975). Whether the explanation for the food-sharing behaviour is kin selection or reciprocal altruism the presence of either factor will reinforce the selective advantage accruing to group foragers.

SOCIAL ORGANIZATION

The results of the radio-tracking study, the ^{65}Zn spraint labelling technique, the trapping programme, the coastal survey and incidental sightings all contributed to a model of the social organization of *Aonyx capensis* in the Tsitsikama Coastal National Park.

RANGE OVERLAP AND CLANS

Trapping data in both van der Zee's (1979) and the present study indicated that adult male ranges overlapped. Van der Zee (1979) trapped a total of five males in the immediate vicinity of the rest camp while four males, all adults, were trapped in the same area during the present study. Van der Zee's (1979) simultaneous capture of two males, one adult and one sub-adult or adult, in the same trap was a further indication of the high level of tolerance of adult males to the presence of other males. The residential status of one of the males trapped by Van der Zee (1979) and the four males trapped in the present study was confirmed by multiple captures of these animals in the vicinity of the rest camp (see Trapping Results).

Radio-tracking results (Fig. 14) provided proof of extensive range overlap between adult males, simultaneous occupation of these ranges and group foraging by adult males. The individual otters sharing a range did not display spatio-temporal territoriality and often denned together. The term clan defined by Kruuk (1978a) as "a group of animals jointly inhabiting an area", was deemed applicable to the social organization of *Aonyx* on the Tsitsikama coast.

The six adult males whose home ranges have been wholly or partially mapped in Figure 14, appear to belong to two groups. The group with the more easterly range, centred on the rest camp, consists of at least four adult males (Eric, Fat Freddy, Dougal and Oleg) and at least one adult female, though this animal could not be confirmed as a resident. Observations confirmed that this group was a clan and it is hereafter known as the Stormsriver clan.

The group with the more westerly range, which is probably not fully mapped, includes two adult males, Naffer and Biggles, known to be resident, an adult female and an immature male, both probably resident. Of these animals, Naffer, the first to be trapped and then radio-tracked was found dead three weeks after his release on 8/9/1981. Biggles was captured inside Naffer's range a month after the last sighting of Naffer. In view of the stability of the Stormsriver clan (see below) it seems likely that Biggles was resident in Naffer's range while the latter was still alive. These two animals are therefore assumed to be members of the same group. Owing to the short period of radio-tracking this group could not be confirmed as a clan. The four animals trapped at the Geelhoutbos are hereafter known as the Lottering group.

The extreme limits of Biggles' range cannot be taken as the extreme limits of the group range owing to the limited period of radio-tracking. The extreme limits of Dougal's range, defined after ten weeks tracking, may be assumed to approximate to the extreme limits of the Stormsriver clan range.

The range utilisation data of Dougal, when combined with the known ranges and movements of Fat Freddy and Eric, suggest the existence of a well defined core area (see Discussion on Range utilisation) within the Stormsriver clan range. This extends from approximately holt 9, just east of Skildekrans to holt 7 at Steilkop. All the above mentioned animals were found on this stretch of coast which is precisely defined by Eric's range illustrated in Figure 14 , and includes sections 37-53 illustrated in Figure 18 . The core area of Dougal's range, subject to a significantly higher level of utilisation than the rest of his range, coincided almost exactly with this, covering sections 38-54. If sections 37-53 are taken as the core area of the clan it extends over 8,5 km of coast.

There is no indication of the existence of a core area for the Lottering group. However this is not surprising in view of the limited period of radio-tracking devoted to Naffer and Biggles. If the group is a clan and has a core area, it probably lies west of the Geelhoutbos River as neither Biggles nor Naffer were ever found east of the Geelhoutbos.

Evidence for overlap of the clan range with the ranges of neighbouring males is provided by Dougal's use of holt 18 at the Geelhoutbos River (Fig. 14). This holt had previously been used by both Naffer and Biggles. If Biggles and Naffer were not captured at the extreme eastern limits of their ranges this overlap is greater than illustrated in Figure 14 .

Repeated visits to the coast between the Geelhoutbos River and Skildekrans, and the spraint densities recorded during the coastal survey, indicated that this section of coast was utilised by otters as heavily as the core area of the Stormsriver clan. The otters of the Stormsriver clan utilised the core area far more heavily than the section between Skilderkrans and Geelhoutbos. The latter section must therefore be utilised by other otters if the overall level of utilisation, as indicated by spraint densities, is equal to that of the Stormsriver clan core area.

Confirmation that otters other than Stormsriver clan members use the coast between the Geelhoutbos River and Skilderkrans was provided by results of ^{65}Zn population estimate technique (see Results and Fig. 9). An adult female and immature male showed heavy utilisation of the coast between the Elandsbos and Skilderkrans but only rarely progressed further east than Skildekrans. These animals were captured at the Geelhoutbos River, made frequent use of part of the known range of Biggles and Naffer, and are therefore members of the Lottering group. However the exact rôle of females and immature males within the social organization of *Aonyx* is not clear as all the available radio-tracking data relate to adult males.

The distribution of radio-actively labelled spraints is also pertinent to territorial behaviour and the full implications of the observed distribution are discussed later in the section on territoriality. For the present it is sufficient to note that there is evidence of substantial overlap between neighbouring clan ranges.

Overlap of ranges has been observed in all coastal populations of otters studied. The overlap observed in sea otter (*Enhydra lutris*) home ranges is the most extensive recorded to date (Loughlin, 1980). However, the social organizations of *Enhydra* and *Aonyx* are radically different, the population density of *Enhydra* is much higher than that of *Aonyx* and consequently the patterns of range overlap observed in the two species are strikingly dissimilar. This variation in social behaviour is probably a response to differences in ecological factors between the two habitats and in the degree to which the two species are adapted for a marine existence. *Enhydra*'s independence of terrestrial resources (e.g. freshwater and holts) obviates factors which might otherwise limit range overlap.

Watson (1978) and Kruuk and Hewson (1978) both found evidence of range overlap in coastal populations of *Lutra lutra*. However there was no evidence for a clan type of social organization in the Shetland population of *L. lutra*, though population density of these otters was apparently higher than that of *Aonyx*. Home range size was much smaller in this *L. lutra* population, that of a female and cub covering only 2,5 km of coast. This compares with the range estimate for one female *Aonyx* of at least 14,3 km of coast (see Population Estimate Results). Available evidence indicates that *L. lutra* population density is similar to that of *Aonyx* (see Discussion on Population Estimate). Given the similar population densities large ranges with greater overlap (*Aonyx*) are an alternative social strategy to small ranges with less overlap (*L. lutra*).

Adult male *L. lutra* studied in a freshwater habitat occupied individual home ranges within which females and cubs occupied a range (Erlinge 1967 , 1968). There was overlap between the ranges of neighbouring males but each had separate centres of activity. As there was no clan system overall range overlap was much reduced in comparison with that seen in *Aonyx*.

The wide variation in ecological factors between a marine and a freshwater habitat, of which only some are identifiable and none quantified, make explanation of observed differences in social organization speculative. However one major difference is in the configuration of the home ranges and the resource dispersion within those ranges. Freshwater populations of *L. lutra* are not restricted to linear home ranges, as is *Aonyx* on the Tsitsikama coast. Food is only available in limited areas within the range of *L. lutra* (the streams and lakes) but is available throughout the coastal range of *Aonyx*. Resource dispersion is therefore radically different in these two habitats and recent studies have shown that this factor is instrumental in determining the spacing and structure of carnivore societies (Macdonald, 1983).

TERRITORIALITY

Inconclusive evidence for territoriality between Aonyx clans was provided by results of the trapping programme and the ^{65}Zn labelling technique.

Trapping between holt 5 and holt 1 (Fig. 18) was conducted on a total of 71 trap-nights (Table 11). In this period five adult otters were caught, four males and one female. All the males were caught at least twice and their status as residents within the Stormsriver clan range was confirmed by radio-tracking. The female was only caught once and never radio-tracked so her residential status could not be confirmed.

The fact that only resident males were caught in this central stretch of the Stormsriver clan range suggests that it is an exclusive area, at least as far as other males are concerned. A higher total of trap-nights might have strengthened the evidence. All known residents were caught at least twice and the high trapping success rate of 16,7% make it likely that any regular intrusions would have resulted in the capture of at least one non-resident male.

The distribution of radio-active spraints deposited by two otters captured at a holt within the range of Biggles and Naffer shows an abrupt discontinuity at Skilderkrans. This indicates that the two labelled otters, an adult female and an immature male, rarely moved east of Skilderkrans into the core area (see Results on Home Range Utilisation and Movement Patterns) of the Stormsriver clan. This is to be expected if the core area of clan is used more or less exclusively by members of that clan.

The radio-tracking results also provide some support for the hypothesis of the core area as a territory. The patterns of movement illustrated in Figure 17 and home range utilisation data illustrated in Figure 20 indicate a sharp delineation between the core area and outlying areas of the clan range. Though clan members do move beyond the core areas these excursions are relatively infrequent and often of short duration (see Results and Discussion on Movement Patterns). This behaviour suggests that there is an established boundary at either end of the core area which is recognised by the Stormsriver clan members.

The majority of the data on social organization refer to males and there is little information available on the rôle of females in clans. Evidence from the ^{65}Zn labelling technique suggests that the core area of a female's range is somewhat smaller than that of the male (see Results on Population Estimate). The only estimate available for total female range size (14,3 km) is less than that of Dougal's (19,5 km). However this female range size is a minimum estimate.

There is no evidence on the location of individual core areas in relation to the core areas of males and other females. An adult female was trapped in the core area of the Stormsriver clan range but the location of her core area was unknown and furthermore her residential status could not be confirmed.

Details of intraspecific signals and interactions whereby territoriality is maintained are not clear. Spraints are undoubtedly scent-marks but it is not known to what extent they serve as territorial signals (see Discussion on Coastal Survey). There is no concentration of spraints at the boundaries of the core area of the Stormsriver clan. Holt 7 at the eastern boundary is associated with a frequently used spraint site (Table 4) but is still subject to periods when no marking at all occurs. Similarly holts 9, 8 and 11 (Fig. 18) near the western boundary of the core area do not appear to be used more frequently or consistently than other holts.

However, as explained in the Discussion of the coastal survey results spraints at holts throughout the range could serve to deter intruders. It may be that the intensity of marking of a holt by members of a clan determines the likelihood of intrusion by a member of a neighbouring clan. Holts in the core area marked frequently by clan members would be subject to infrequent intrusion whereas those in the area of overlap used and marked less frequently by the clan are also used and marked regularly by the neighbouring clan.

The only recorded incidence of intraspecific aggression in *Aonyx* may have been linked to territoriality as it occurred within the core area of the Stormsriver clan range. The two otters observed attacking a lone animal may have been engaging in cooperative defence of territory. The fact that the fight involved three animals and was not just a dispute between two individuals is particularly significant. Cooperative defence has been recorded in several social species such as spotted hyaenas (Kruuk, 1972) and red foxes (Macdonald, 1977). As the identity of none of the otters was known, this hypothesis could not be confirmed.

The adaptiveness of territoriality as a behavioural strategy depends on the balance between the costs and benefits of priority of access to a resource i.e. the economic defendability of the resource (Brown, 1964). The critical resource or resources were not identified, but it is worth noting that the linear configuration of the clan range and aquatic habits of *Aonyx* are likely to influence resource defendability. As *Aonyx* is restricted to the coast intrusions into the range will be concentrated at opposite ends of the range. Maintenance of such widely spaced territorial boundaries under these conditions would impose a high energetic cost on a single animal. Boundaries in the marine foraging areas cannot be established by marking behaviour so that exclusion of intruders from areas would depend on encounters with residents. It may only be the reluctance of an intruder to use a holt heavily marked by other otters that minimises foraging intrusions into the clan core area.

Cooperative defence by a social group, members of which can be in different places at the same time, will reduce the cost of territoriality to an individual and probably also increase the effectiveness of territorial defence. Whereas one individual would have to commute continuously between the opposite ends of his territory, a clan of say four animals, foraging individually or in sub-groups, may be able to maintain such widely spaced boundaries in the course of their normal foraging activities. Thus it may be that the linear nature of the marine habitat has been an important factor in the evolution of the social organization of *Aonyx* in the Tsitsikama Coastal National Park.

MANAGEMENT RECOMMENDATIONS

Van der Zee (1979) essentially recommended that management action with regard to the Tsitsikama Coastan National Park *Aonyx* population be based on minimal interference. The present study has confirmed that the population density of *Aonyx* is similar to that in other coastal populations of otters, with the exception of the true sea otter, *Enhydra lutris*, and there is no reason to alter this recommendation.

However in view of the further development of tourist facilities at Storms River Mouth and the increase in tourist pressure both in the rest camp and on the Otter Trail it would be wise to lay more stress on van der Zee's (1979) recommendation to minimise human disturbance within the rest camp. Human disturbance has taken the form of damage to the indigenous shrubs which provide the necessary cover for the establishment of holts. Since van der Zee's study the utilisation of holts 2 and 35 has dropped considerably. The cover at holt 2 is very fragmentary at present and holt 35 has been encroached upon by two of the more popular camping sites. Conservation of such patches of bosh should become a priority if otters are to continue using holts within the rest camp. Though loss of these two holts would not seriously affect the Tsitsikama otter population, the regular appearance of otters within the rest camp serves to demonstrate to the public the effectiveness of the conservation measures in the Park.

McDonald, Mason & Coghill (1978) stressed the European otter's requirement for dense cover in the immediate vicinity of their aquatic habitat, when making management recommendations.

With respect to the Otter Trail the only possible measure is to brief tourists on the effects of human disturbance on *Aonyx*. More noise and more damage to the bush at holts will result at best in more wary and less visible otters. The location of the holt near André's hut should not be given in the Otter Trail briefing.

Both these recommendations apply to otter populations outside nature reserves, especially the minimisation of damage to patches of bush which provide dense cover. At Oubosstrand just east of the eastern boundary of the Park, clumps of dense bush within the village were heavily utilised by *Aonyx*. Streams running through this village were apparently unpolluted, conservation of such freshwater supplies being another requirement for the maintenance of coastal otter populations (van der Zee, 1979). The importance of maintaining otter populations outside nature reserves cannot be over-stressed. The Tsitsikama population of only 31 otters would not be viable in the long term if it existed in isolation.

Maintenance of viable populations of *Aonyx* along the coast undoubtedly depends to a large extent on the conservation of prey populations in the littoral and sub-littoral zone. Such conservation is apparently very effective in the Tsitsikama Coastal National Park and the otter population density here is higher than recorded anywhere else on the South African coast.

The large range covered by adult *Aonyx*, revealed by radio-tracking and the ^{65}Zn labelling technique, indicates the necessity of large reserves for the conservation of *Aonyx*. In the case of an adult male such as Dougal, at least 20 km of coast would have to be included in a reserve to provide protection for the animal throughout his range. In terms of the conservation of *Aonyx* isolated reserves smaller than the Tsitsikama Coastal National Park are likely to be of little value. Ideally reserves the size of this Park should be scattered at intervals along the coast, separated by areas in which at least some measures are taken to protect indigenous bush, freshwater supply and the littoral habitat. A few such larger reserves will serve the purpose far better than many small ones. This recommendation conforms to the general rule for the design of nature reserves developed as a result of studies in island biogeography (May, 1975).

CONCLUSIONS

A population of about 31 otters using 120 holts exists within the Tsitsikama Coastal National Park. Maintenance of the present levels of protection within the Park and the continued presence of potential immigrants on the coast immediately outside the Park should ensure the future of the Tsitsikama population.

The variation in the composition of the diet of *Aonyx* in two separate areas within the Park indicates that it is not safe to generalise about the feeding ecology of *Aonyx* on the basis of a study conducted in only one section of the Park. The importance of crabs in the diet of *Aonyx* at Tsitsikama appears to have been overestimated in view of the major calorific contribution of fish species.

Radio-tracked adult males were predominantly nocturnal, a behavioural attribute that renders *Aonyx* more resistant to human disturbance than predators with diurnal habits. In areas where full protection is deemed necessary to ensure the continued existence of the local *Aonyx* population, reserves incorporating long stretches of coast will have to be proclaimed to accommodate the extensive ranges utilised by individual otters.

The clan type of social organisation which apparently incorporates a degree of territoriality indicates that the local population density of *Aonyx* may be limited by social behaviour. As a result translocation of animals may prove ineffective as a conservation measure.

SUMMARY

The predominantly nocturnal habits and elusiveness of Aonyx capensis in the Tsitsikama Coastal National Park dictated the methods used in the study - many of the data were obtained by the examination of tracks and sign, while prolonged observation was only achieved by the use of radio-tracking techniques.

One hundred and twenty holts were located in the 58,5 km of coast included in the Park. The density of holts was slightly higher and the density of spraints (faeces) significantly higher in the eastern half of the Park.

There is temporal variation in the levels of utilisation of individual holts and variation in the mean levels of utilisation between holts.

Mean nearest neighbour distance between holts was 350 m and the mean inter-holt distance was 470 m. Distribution of holts along the coast is non-random, there being a tendency towards even spacing. All holts were located in dense bush and were almost invariably associated with a supply of fresh water.

56,2% of spraint sites and 85,4% of spraints located during the coastal survey were within 50 m of a holt. The concentration of spraints close to holts is not unexpected in view of the fact that Aonyx rarely comes ashore except in the vicinity of holts.

The proportions of fish and crab in the diet of Aonyx, estimated from the analysis of prey remains in spraints, shows considerable variation between two separate sections of coast. At least three of the fish species taken by Aonyx have much higher calorific values than the two

crab species. In view of the higher proportion of assimilable biomass in fish it would appear that their importance in the diet of *Aonyx* on the Tsitsikama coast has been underestimated.

A total of eight males and four females were trapped in standard caracal traps at ten sites inside and outside the Park. The trapping data are not a reliable indication of the sex ratio in the Tsitsikama population of *Aonyx* as there was evidence to suggest that adult females with cubs never enter traps.

Four animals were trapped at least twice and overall success rate was 16,7% (16,7 otters per 100 trap-nights). Problems were encountered in marking the animals for field recognition as dye marker and all ear tags, except small aluminium fish tags, only visible at short range, were ineffective. Temporary marking was achieved by shaving a small patch of hair on the haunch.

The dimensions of otters trapped during the two studies in the Tsitsikama Coastal National Park do not differ significantly from those of *Aonyx* specimens caught in inland areas.

Two adult females and an immature male received intramuscular injections of $^{65}ZnCl$ which resulted in the radio-active labelling of their spraints. The proportion of radio-actively labelled spraints in samples collected either side of the release sites of these otters provided estimates of the population density of *Aonyx*. In an area west of Stormsriver there were approximately 0,50 otters km^{-1} of coast and in an area east of Stormsriver there were approximately 0,54 otters km^{-1}. The estimate of population size for the whole Park was 31 otters. The distribution of labelled spraints originating from an adult female indicated a minimum range size of 14,3 km of coast. There was an area of peak utilisation 5,7 km long towards the centre of this range. The distribution of labelled spraints originating from an adult female and immature male indicated that they avoided the neighbouring core area of the range of four adult males.

Five adult males and one adult female trapped in the course of the study received intraperitoneal implants of radio transmitters. All the data presented refer only to the five adult males and most were obtained from only three of these animals.

Aonyx in the Tsitsikama is predominantly nocturnal. A male tracked during the summer showed the greatest proportion of nocturnal activity and one tracked during the winter the greatest proportion of diurnal activity. The peak of activity occurred between 20h00 and 22h00 - after sunset in all seasons. Minimum activity levels occurred between 04h00 and 06h00 and again between 10h00 and 16h00. Bouts of foraging activity had a mean duration of 70 minutes, and an otter would conduct three to five such forays in the course of a night.

The ranges of five adult males were at least partially mapped. One adult male which traversed a minimum of 19,5 km of coast was radio-tracked for long enough to ensure that this estimate approximated to his full range. The home range of this animal was estimated as 15 km of coast or 150 ha of water surface. Three other adult males had minimum ranges of 8,6 - 13,3 km of coast but none of these animals were tracked for more than three weeks.

An 8,5 km central section of the range of the former animal was utilised to a significantly greater extent than the remainder of his range. This section of coast corresponds to the entire known range of one other adult male and the majority of the known range of a third. This area of intense utilisation was designated a core area after Kaufmann (1962). Within this core area there were separate localised peaks of utilisation for two of these adult males.

Otters displayed individual preferences for particular holts, the location of which coincided with their favoured foraging areas. Foraging activity was apparently not restricted by sea conditions or the stamina of *Aonyx*. The speed in the water of a foraging otter during summer was positively correlated and that of another animal in winter negatively correlated with sea temperature. Two adult males tracked in autumn and summer displayed a preference for foraging at low tide and avoided high tides. The reverse was true for another adult male tracked in winter.

Success rates of foraging dives of *Aonyx* foraging alone and in groups was similar, being 62% and 59% respectively. There was no indication that crabs and fish were caught in different proportions by group and solitary foragers.

Pairs of adult males and groups of three including at least two adult males were observed to forage together. Animals were seen to dive and surface in synchrony and may have been hunting cooperatively. On one occasion two adult males were seen to share a prey item that was caught by only one of the pair.

There is evidence to suggest that male foraging groups only form between April and September. Radio-tracked adult males observed between October and March were invariably solitary.

Aonyx on the Tsitsikama coast appeared to have a clan-type of social organisation. Four adult males shared a common range and the holts within it and members of this Stormsriver clan were seen to forage together on several occasions. The 8,5 km core area of the adult male with a 19,5 km range (see above) appeared to be a core area for the clan. Evidence from trapping data and the ^{65}Zn labelling technique suggested that non-clan members avoided entering the clan core area which therefore appears to be a territory. Areas immediately outside the core area are used by clan members and non-clan members alike. One adult female was trapped within the core area of the Stormsriver clan.

Marine reserves proclaimed to protect local populations of *Aonyx* should be at least of a similar size to the Tsitsikama Coastal National Park (58,5 km of coast). However, conservation of the littoral and sub-littoral habitat, freshwater supply and bush along coasts should ensure the future of coastal populations of *Aonyx*.

OPSOMMING

Omdat Aonyx capensis in the Tsitsikamaseekus Nasionale Park hoofsaaklik gedurende die nag aktief is en ook skugter van geaardheid is is die meeste inligting verkry deur die navolging van spore en ander tekens van aktiwiteit. Langtermyn waarnemings was slegs moontlik deur die gebruik van radio-opsporingstegnieke.

Eenhonderd-en-twintig skuilplekke is oor 'n afstand van 58,5 km langs die kus binne die Park opgespoor. Die digtheid van skuilplekke was effens hoër en die digtheid van mis betekenisvol hoër in die oostelike gedeelte van die Park.

Die intensiteit van verbruik van spesifieke skuilplekke het met verloop van tyd gewissel en die gemiddelde vlak van benutting van verskillende skuilplekke varieer ook.

Die gemiddelde afstand tussen naasliggende skuilplekke was 350 m en die gemiddelde interskuilplek-afstand was 470 m. Skuilplekke is nie ewekansig langs die kus versprei nie maar daar was 'n neiging tot eweredige verspreiding. Alle skuilplekke was in digte bosse en was deurgans naby vars water.

56,2% van alle misplekke en 85,4% van al die mishope wat gedurende 'n opname langs die kus opgespoor is was binne 50 m van 'n skuilplek. Die groot hoeveelheid mishope naby skuilplekke is te wagte omdat Aonyx gewoonlik naby die skuilplekke aanwal kom.

Die verhouding van visse en krappe in die dieet van Aonyx soos bepaal deur die analiese van prooi-oorblyfsels en mis, verskil in twee gebiede wat langs die kus ondersoek is. Die energie-inhoud van ten minste drie van die vissoorte waarop Aonyx voed is hoër as dié van die twee krapsoorte in die dieet. As gevolg van die groter verhouding van verteerbare biomassa in visse blyk dit dat die belang van vis in die dieet van Aonyx langs die Tsitsikamakus onderskat is.

Agt mannetjies en vier wyfies is met behulp van rooikatvalle op tien lokaliteite binne en buite die Park gevang. Hierdie inligting is nie 'n betroubare weergawe van die geslagsverhouding van die bevolking nie omdat volwasse wyfies met kleintjies skynbaar nooit valle binnegaan nie.

Vier otters is ten minste twee maal gevang en die algemene vangsukses was 16,7% (16,7 otters per 100 valnagte). Probleme is ondervind met die merk van otters vir identifisering in die veld. Kleurmerk en oorplaatjies met die uitsondering van klein aluminium kenplaatjies wat vir visse gebruik word en wat gevolglik slegs op 'n kort afstand sigbaar was, was oneffektief. Gevolglik is otters tydelik gemerk deur 'n klein gedeelte van die hare op die kruis af te skeer.

Die liggaamsmates van otters wat gedurende die twee studies in die Tsitsikamaseekus Nasionale Park gevang is verskil nie betekenisvol van individue van dieselfde spesies wat in die binneland gevang is nie.

Twee volwasse wyfies en 'n onvolwasse mannetjie is binnespiers met $^{65}ZnCl$ ingespuit en sodoende is hulle mis gemerk met die radio-aktiewe stof. Mismonsters is van beide kante van die punt van vrylating van hierdie diere versamel en die verhouding gemerk tot ongemerkte monsters is gebruik vir die bepaling van bevolkingsdigtheid. Digtheid vir 'n gebied wes van die Stormsrivier was ongeveer 0,50 otters km^{-1} kuslyn en vir 'n gebied oos van die rivier ongeveer 0,54 otters km^{-1} kuslyn. Bevolkingsgrootte vir die Park as 'n geheel was 31 otters. Die verspreiding van gemerkte mishope van 'n volwasse wyfie dui daarop dat die minimum lengte van haar tuisgebied 14,3 km kuslyn was. 'n Gebied van 5,7 km aan weerskante van die middel van die loopgebied is meer intensief as die res daarvan gebruik. Die verspreiding van gemerkte mishope van 'n volwasse wyfie en die onvolwasse mannetjie het aangetoon dat hulle die aangrensende kerngebied van vier volwasse mannetjies se loopgebied vermy het.

Vyf volwasse mannetjies en 'n volwasse wyfie is gedurende die verloop van die studie intraperitoneaal met radiosenders voorsien. Al die inligting wat hier aangebied word is verkry van die vyf volwasse mannetjies en hoofsaaklik van drie van hierdie diere.

Otters in die Tsitsikama is hoofsaaklik gedurende die nag aktief. 'n Mannetjie wat gedurende die somer gevolg is was meer aktief gedurende die nag terwyl een wat gedurende die winter gevang is in die dag meer aktief was. Die piek in aktiwiteit was tussen 20h00 en 22h00 gedurende al die seisoene. Laagtepunte in aktiwiteit het tussen 04h00 en 06h00 en weer tussen 10h00 en 16h00 voorgekom. Die gemiddelde lengte van die tydperke waarin kos gesoek is was 70 minute en 'n otter sal drie tot vyf keer per nag so voedsel soek.

Die loopgebiede van vyf mannetjies is gedeeltelik gekarteer. Een van hierdie otters het oor 'n minimum afstand van 19,5 km langs die kus beweeg en is lank genoeg gevolg om seker te maak dat hierdie waarde sy totale gebied verteenwoordig. Die tuisgebied van hierdie dier is verteenwoordig deur 'n kusstrook van 15 km of 'n wateroppervlakte van 150 ha. Drie van die ander mannetjies het beweeg oor 'n gebied van 8,6 - 13,3 km kus maar nie een van hierdie otters is vir langer as drie weke gevolg nie.

'n Sentrale gedeelte van 8,5 km van die gebied van die eerste mannetjie is betekenisvol meer intensief gebruik as die res van die gebied.

Hierdie gedeelte van die kus het die totale bekende gebied van een ander volwasse mannetjie en die grootste gedeelte van die gebied van 'n derde mannetjie ingesluit. Volgens die definisie van Kaufman (1962) kan hierdie gebied van intense gebruik gedefinieer word as die kerngebied. Binne hierdie gebied was daar twee verskillende gelokaliseerde gebiede wat deur twee van hierdie mannetjies gebruik is.

Otters het individuele voorkeur vir spesifieke skuilplekke waarvan die lokaliteit ooreenstem met die gebiede waar voedsel gesoek word. Jagaktiwiteite was oënskynlik nie beperk deur seetoestande of die stamina van die otters nie. Die spoed waarteen deur die water beweeg word was gedurende die somer positief en gedurende die winter negatief gekorreleer met seetemperature. Twee volwasse mannetjies wat gedurende die herfs en somer gevolg is het hoofsaaklik gedurende hoogwater kos gesoek en hoë getye is vermy. Die teenoorgestelde was gevind by 'n mannetjie wat gedurende die winter gevolg is.

Die tempo van sukses wanneer geduik word om kos te soek was dieselfde vir enkel diere as vir groepe diere en was respektiewelik 62% en 59%. Geen aanduidings kon gevind word dat die verhouding van krappe tot visse wat deur groepe en enkel diere gevang word verskil nie.

Groepe bestaande uit twee volwasse mannetjies en groepe bestaande uit drie diere waarvan ten minste twee volwasse mannetjies was het saam kos gesoek. Otters is waargeneem om saam to duik en weer saam na die oppervlak te kom; hierdie sinkronisasie word vertaal as saamjag. Twee volwasse mannetjies het eenmaal prooi wat deur een van hulle gevang is gedeel.

Die beskikbare gegewens dui aan dat groepe mannetjies net tussen April en September gesamentlik jag. Alle mannetjies wat tussen Oktober en Maart waargeneem is was alleenlopend.

Otters langs die Tsitsikamakus het waarskynlik 'n stamgroep-tipe van sosiale organisasie. Vier volwasse mannetjies het 'n gemeenskaplike loopgebied sowel as skuilplekke gedeel en lede van die Stormsrivier stamgroep het dikwels saam gejag. Die kerngebied van 8,5 km van die mannetjie wat 'n loopgebied van 19,5 km gehad het verteenwoordig waarskynlik die kerngebied van die groep. Inligting verkry deur die vang en merk van otters asook deur middel van ^{65}Zn, dui aan dat diere wat nie lede is van 'n groep nie die sentrale gebied van die groep vermy. Hierdie gebied verteenwoordig waarskynlik die territorium van die groep. Die omringende gebied word deur lede van die groep sowel as ander otters gebruik. Een volwasse wyfie is in die sentrale gebied van die Stormsriviergroep gevang.

Kusreservate wat geproklameer sou word om lokale otterbevolkings te beskerm behoort ten minste dieselfde grootte as die Tsitsikamaseekus Nasionale Park (58,5 km kuslyn) te wees. Die beskerming van die littorale en sub-littorale habitat, varswaterbronne en bebosde gebiede langs die kus behoort die toekoms van otterbevolkings te verseker.

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APPENDIX I

INFORMATION ON TICKS COLLECTED FROM *AONYX CAPENSIS* TRAPPED ON THE TSITSIKAMA COAST, FURNISHED BY MISS J.B. WALKER, VETERINARY RESEARCH INSTITUTE, ONDERSTEPOORT

A total of 102 specimens of *Ixodes corwini* (47 females, 5 males and 50 nymphs) were collected from twelve trapped otters. This species is a member of the *Ixodes oldi* group, representatives of which Miss Walker previously identified in a collection made by Douwe van der Zee (1979). Other known hosts of this tick in the Cape Province are *Herpestes pulverulentus*, *Herpestes sanguineus*, *Genetta genetta* and *Genetta tigrina*.

One female *Ixodes pilosus*, the sourveld tick, was also collected. This species has been recorded from a wide range of both domestic and wild animals, and is particularly common on the coast between Port Shepstone and Cape Town.

Two male *Haemophysalis spinulosa* were identified in the collection. This species is a parasite of the small carnivores of which little is known.

Twenty-nine larvae of the genus *Ixodes* were also collected. These were probably *I. corwini*.