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New frog records from the Eastern Caprivi Strip, South West Africa/Namibia

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ABSTRACT

A survey of the Eastern Caprivi Strip, SWA/Namibia, during January to March 1986 resulted in the collection of 26 species of anurans, of which four are new records for the country. *Ptychadena cotti*, *Ptychadena taenioscelis*, *Ptychadena upembae* and *Phrynobatrachus stewartae* are known from north and east of the area, and demonstrate a link with the tropical frog fauna in Malawi. An annotated list of species collected from the Eastern Caprivi Strip is presented.

INTRODUCTION

Frogs are an important link in the food web supporting some of the larger birds and carnivores. Platannas (*Xenopus* sp.) are eaten by local tribesmen in central Africa and the African bullfrog features in the diet of many African tribes. Frogs are a convenient ecological indicator, being relatively widespread, and adapted to a range of habitats. A knowledge of the frog fauna of an area is a necessary prerequisite in the planning of any conservation strategy.

The geographical location of SWA/Namibia on the southwestern coast of Africa, results in an interesting and varied frog fauna composed of tropical species in the northern savanna areas, arid-area adapted species in the Namib desert and adjacent drylands, and a few Cape species (Poynton 1964) which extend into the south of the country.

The Eastern Caprivi Strip lies on the northeastern border of the country at an altitude of about 930 m above sea level, and the eastern flood plain is usually inundated by the Zambezi River from February to June (Van der Waal & Skelton 1984). The combination of warm temperature and regular flooding produce an area with great potential for studies on anuran amphibians.

This paper lists four new SWA/Namibia records of anuran amphibians collected during an initial survey, January to March 1986 in the Eastern Caprivi Strip. An annotated list of all the frog species collected during the initial survey is also presented.

COLLECTION AND IDENTIFICATION

Collecting was carried out by repeated visits to various habitats near Katima Mulilo, and infrequent trips to Nkasa Island in the southwestern corner of the area, and elsewhere. Eggs and tadpoles were located during daytime visits, while adults were found after dark. Breeding choruses were noted, and tape recordings made of representatives of all species calling.

Identifications of the four species new to the area were

based on the descriptions and keys in Poynton and Broadley (1985b), and on the sonagrams of the advertisement calls of the male frogs in Passmore and Carruthers (1979). The identifications of all the species collected during this survey were checked using standard works for adults (Poynton 1964; Channing & Van Dijk 1976; Poynton & Broadley 1985a, b, 1987) and tadpoles (Van Dijk 1966; Channing & Van Dijk 1976). Nomenclature follows Frost (1985).

Advertisement calls were analysed on a Kay 7029A Sonagraph. The male advertisement call is a powerful taxonomic tool, as it is part of each frog species' specific mate recognition system (Passmore & Carruthers 1979), and can serve as a positive method of identification. The calls of species whose range extends into South Africa were compared to the sonagrams in Passmore and Carruthers (1979). A gazetteer of all the localities where specimens were collected is given in Table 1. All specimens of adults collected have been deposited in the State Museum, Windhoek, and the California Academy of Sciences, USA.

Table 1. Gazetteer of the localities mentioned in the text

Locality	Latitude / Longitude
Chinchimane	17 56'S / 24 10'E
Chinchimane road	17 58'S / 24 08'E
Chobe river	17 53'S / 24 46'E
Ihaha	17 49'S / 24 52'E
Kasika	17 48'S / 25 06'E
Katima Mulilo	17 32'S / 24 15'E
Katima Mulilo, 13 km west	17 32'S / 24 15'E
Katima Mulilo, 20 km west	17 33'S / 24 18'E
Katima Mulilo, 10 km south	17 37'S / 24 15'E
Lake Liambezi	17 55'S / 24 23'E
Lake Lisikili	17 33'S / 24 39'E
Liambezi floodplain	17 52'S / 24 23'E
Lusese	17 43'S / 24 47'E
Maningimanzi	17 30'S / 24 23'E
Mpacha	17 38'S / 24 10'E
Mufalali	18 15'S / 23 30'E
Mutwalwezi	17 44'S / 24 50'E
Nkasa Island	18 26'S / 23 39'E
Old Sangwali	18 20'S / 23 43'E

NEW FROG RECORDS

Ptychadena cotti (Parker) 1930

Synonymies: See Poynton and Broadley (1985b).

New records: Katima Mulilo, Mpacha.

Comment: Nearest previous record Malawi. This range extension suggests that many other species with predominantly tropical distributions may yet be recorded from SWA/Namibia. These frogs are found in very dense vegetation at the edge of shallow pools. They occur with *Ptychadena anchietae* and *Ptychadena mascareniensis*. The male advertisement call is presented in Figure 1A.

Ptychadena taenioscelis Laurent 1954

Synonymies: See Poynton and Broadley (1985b).

New records: Nkasa Island.

Comment: Males call from short flooded grass. The advertisement call of the Caprivi Strip specimens (Figure 1B) is similar to that shown in Passmore and Carruthers (1979).

Ptychadena upembae (Schmidt and Inger 1959)

Synonymies: See Poynton and Broadley (1985b).

New records: Nkasa Island.

Comment: Males call from concealed positions in thick grass or under debris within 50 cm of shallow water in pans. These frogs are very difficult to locate, which may partly explain why they have not previously been recorded from SWA/Namibia. The advertisement call is shown in Figure 1C.

Phrynobatrachus stewartae Poynton and Broadley, (1985b)

Synonymies: See Poynton and Broadley, (1985b).

New records: Nkasa Island, Katima Mulilo.

Comment: Previously known only from the type locality in Malawi, the Nkasa record is a female collected along the edge of a waterway in short vegetation.

Phrynobatrachus mababiensis was calling in the immediate vicinity. A series was collected at Katima Mulilo in wet weather. The type was described from Malawi, and although the Caprivi Strip specimens are superficially similar to *P. natalensis* (which is also present in the area), they are unambiguously identified as *P. stewartae* using the key in Poynton and Broadley (1985b). The call is unknown.

EASTERN CAPRIVI STRIP RECORDS

The following is a list of all the anuran species collected during this survey. A complete checklist to the frogs of SWA/Namibia is in preparation. Not all the species present in this area were collected. *Leptopelis bocagei*, for example, was heard calling near Katima Mulilo, but could not be located. *Schismaderma carens* had apparently bred early in the season, as only juveniles were found. A collection needs to be made at the start of the rainy season, to investigate the presence of species which breed early in the season.

Bufo gutturalis: Males call along the banks of the Zambezi River, and inland. Eggs were found 6 January 1986 in pool near river. Males called at Nkasa Island 17–19 February 1986. Adults were collected from Katima Mulilo, Lake Liambezi, Mutwalwezi and Nkasa Island.

Bufo maculatus: Males called from the edge of the Zambesi, especially strongly during a dry spell at the end of January, 1986. Adults were collected from the bank of the Zambezi River at Katima Mulilo, and at Mutwalwezi.

Bufo poweri: Juveniles common in wooded areas. Tadpoles were collected from Maningimanzi and near Katima Mulilo. Adults collected from Katima Mulilo.

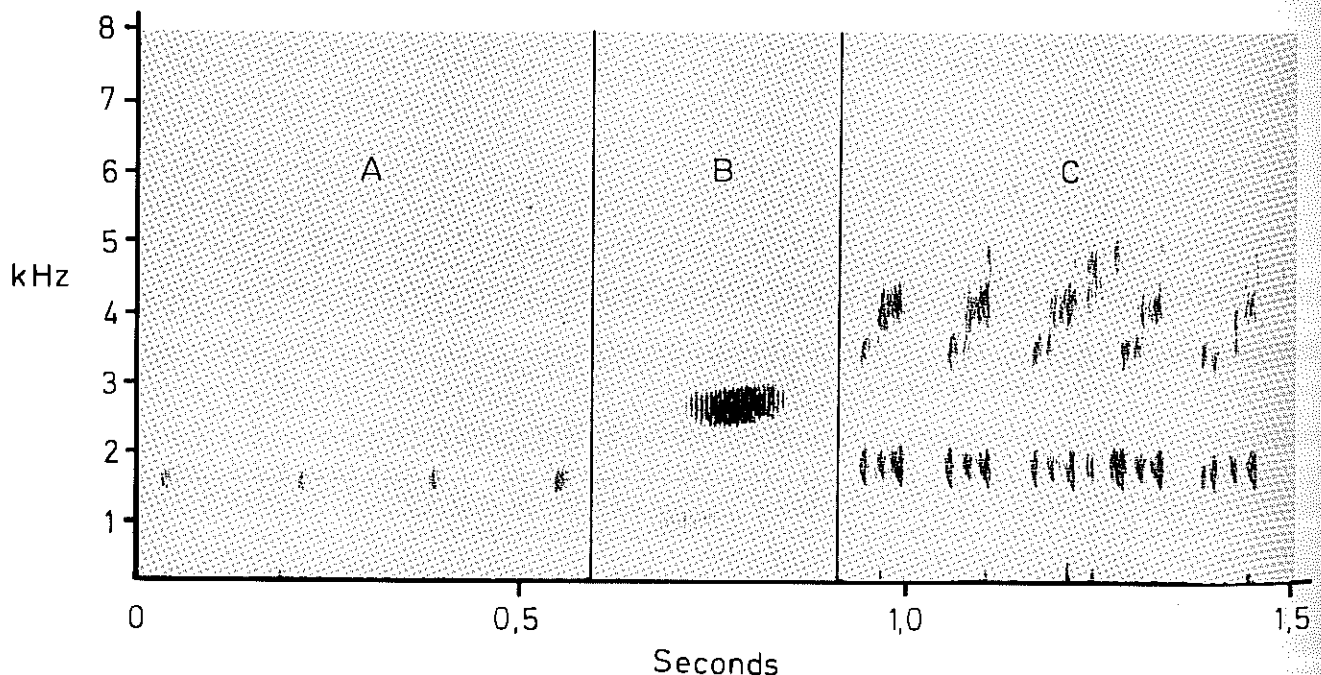


Figure 1. Sonograms of the male advertisement calls of *Ptychadena cotti* (A), *Ptychadena taenioscelis* (B), and *Ptychadena upembae* (C). There is a band of insect noise at 4.5 kHz. The calls of two individuals are visible from the 1.2 s mark onwards.

Bufo vertebralis: Calling at old golf course, Katima Mulilo, 11 January. Males call while clinging to grass over shallow water. Call identical to that in Passmore and Carruthers (1979). Adults collected from Katima Mulilo.

Chiromantis xerampelina: The characteristic foam nests made by this species are very conspicuous. Adults were frequently found during the day near nests. The tadpoles remain in the nest about four days: A fresh nest was collected 16 January and placed over a dish of water. The dish was full of external gill-stage tadpoles on the morning of 20 January. Many larvae at early stages were in the dish, suggesting that the contents of the nest are released simultaneously. One pair of frogs made three nests on three successive nights in captivity. Adult frogs were collected from Katima Mulilo and Lake Liambezi. Tadpoles were collected from Katima Mulilo.

Hemisus marmoratum: Adults could be collected by digging them out of muddy depressions near water during the day. Many newly metamorphosed froglets were collected on roads and in pools during rain 24 January and 9 February 1986. Adults were collected from Katima Mulilo, while tadpoles were collected from 20 km west Katima Mulilo, Katima Mulilo, and Chinchimane road.

Hyperolius aposematicus: Synonymies include *H. angolensis* (Poynton 1964) and *H. marmoratus angolensis* (Poynton & Broadley 1987). These brightly coloured frogs were collected from vegetation away from water during the day. Males were calling from vegetation over deep water at Lake Lisikili 9 February 1986. One pair laid eggs in captivity 10 February. Tadpoles were collected from the banks of the Zambezi River (17°31'E, 24°20'E), while adults were collected from Katima Mulilo, Lake Lisikili, Nkasa Island and Mutwalwezi.

Hyperolius nasutus: This species is found associated with permanent water. Male advertisement calls were recorded from Lake Lisikili and Nkasa Island. The call site is similar to that of *H. aposematicus*, and the two species were always sympatric. Adults were collected from Chobe river, Ihaha, Lake Lisikili, Mufalali, Mutwalwezi and Nkasa Island.

Kassina senegalensis: This ubiquitous African frog is also very common everywhere in the Eastern Caprivi Strip. Males are very difficult to locate, as they call from cracks in mud and other well concealed sites. Tadpoles were collected from 20 km west of Katima Mulilo, Katima Mulilo, and the Liambezi floodplain, while adults were collected from Katima Mulilo.

Phrynobatrachus mababiensis: Males call near water in grass. Emerging froglets were collected 16 January and 3 February 1986. Tadpoles were collected near Katima Mulilo, and adults were collected at Katima Mulilo and Nkasa Island.

Phrynobatrachus natalensis: A batch of tadpoles was metamorphosing and emerging at the old golf course,

Katima Mulilo, on 16 January. Males call during wet and dry weather. Eggs found 17 January, which hatched three days later. Tadpoles were collected from Katima Mulilo, and adults were found at Katima Mulilo and Lusese.

Phrynobatrachus stewartae: This species is similar to *P. natalensis*, but easily distinguished on the amount of webbing (Poynton & Broadley 1985). Adults were collected from Katima Mulilo and Nkasa Island.

Phrynomerus bifasciatus: Males call from concealed positions in or under logs or stumps, or under vegetation. Calling tends to tail off between one rain and the next. Tadpoles were found in nearly every body of water, from large permanent water holes, to temporary pools formed in elephant footprints. Tadpoles were collected from various pools around Katima Mulilo, also 13 km west and 10 km south of the town.

Ptychadena anchietae: Males collected from the bank of the Zambezi River at Katima Mulilo, 17 January 1986. Found in association with *Ptychadena mascareniensis*. Tadpoles collected from Katima Mulilo, in shallow muddy pools

Ptychadena cotti: Adults collected from Katima Mulilo, and 5,7 km south of Katima Mulilo. Eggs and tadpoles unknown.

Ptychadena mascareniensis: Collected from the edge of the Zambezi, and inland. The males call from the bank, under vegetation or exposed. One was found calling in thick grass in a pool, at water level. The advertisement call is identical to that in Passmore and Carruthers (1979). Adults are extremely secretive and difficult to find. A heavy rain 24 January 1986 (38 mm) caused many large choruses to form around Katima Mulilo. Eggs were found 25 January. Adults and tadpoles were collected from Katima Mulilo (old golf course), while adults were collected from Nkasa Island where they were calling 17–19 February 1986 after a heavy rain, and Lake Liambezi.

Ptychadena mossambica: Collected an adult from a water pit at Lake Liambezi. Also very common around Katima Mulilo, many collected from lawns in the town.

Ptychadena oxyrhynchus: In this survey known only from a small collection of tadpoles from 20 km west of Katima Mulilo.

Ptychadena subpunctata: Found mainly in the southern parts, in more open grassland. Adults collected from Kasika in long grass, and others collected at Nkasa Island and Mutwalwezi. Calls recorded 17–19 February at Nkasa.

Ptychadena taenioscelis: Males call from short flooded grass. Collected adults at Nkasa Island after heavy rain.

Ptychadena upembae: Collected from Nkasa Island 17–19 February. Males call from concealed sites near the edge of flooded area in grass.

Pyxicephalus adspersus: Many newly metamorphosed froglets were found hopping near all the water bodies around Katima Mulilo 11 January 1986. By 23 February there were many individuals over 60 mm snout-vent length. Remarkably, no calls were heard at Katima Mulilo from January to March 1986, although they were breeding in the Western Caprivi Strip in February. Only collected from Katima Mulilo (tadpoles and adults).

Schismaderma carens: Uncommon, only four subadult individuals being collected in three months from Katima Mulilo.

Tomopterna cryptotis: Many calling near Katima Mulilo. The tadpoles were usually associated with tadpoles of *Hemisis marmoratum*. Tadpoles and adults collected from Katima Mulilo.

Xenopus muelleri: Tadpoles were collected from 20 km west of Katima Mulilo, Katima Mulilo and Chinchimane. Adults were collected from fish nets at Katima Mulilo, Chinchimane and Old Sangwali.

Xenopus laevis: Only one specimen was collected, after it had hopped into a house in Katima Mulilo during a heavy rain 24 March 1986.

DISCUSSION

Haacke (1970) updated the list of known anuran species in South West Africa/Namibia by the addition of four taxa. The most recent checklist of the frogs of SWA/Namibia listed 30 species (Channing & Van Dijk 1976), one of which (*Strongylopus grayii*) was based on a misidentification of tadpoles (Channing 1979). Jurgens (1979) reviewed the distributions and taxonomy of the frogs of the Etosha National Park. Poynton and Broadley (1985a, b, 1987) have reviewed museum records for the Caprivi Strip.

The new records reported here are all species whose closest known ranges are in Malawi. *Ptychadena upembae* is also known north and east of the Caprivi. The anuran faunas in central Africa are poorly known, and many tropical species will probably still be discovered in the northern part of SWA/Namibia. The importance of perennial rivers as distribution routes into Namibia for species relying on permanent water has been noted by Haacke (1970). The valleys of the Shire and Zambezi Rivers may serve as dispersal routes

for terrestrial species from eastern Africa, while the rich fauna of the Angolan highlands is linked to SWA/Namibia by the river valleys of the Cunene, Cubango, Cuito and Kwando Rivers.

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On the inheritance of the red colour in the Mozambique Tilapia *Oreochromis mossambicus*

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ABSTRACT

Several options for the inheritance of the red colour in the Mozambique tilapia, *Oreochromis mossambicus* are discussed. Breeding with only red mutants resulted in 100% red progeny, while crossing typically coloured individuals and red mutants provided silvery coloured offspring. Interbreeding this offspring resulted in a mixture of red, red typical and typical coloured individuals. It is obvious that the red colour is not due to albinism nor is it the result of a single recessive gene. It is more likely the result of multiple gene interaction, involving several structural genes and at least one regulatory gene. The fact that this mutant breeds pure red makes it, for conservational purposes, a useful substitute for the red tilapia hybrid.

Verskillende opsies vir die oorerwing van die rooi kleur by die bloukurper, *Oreochromis mossambicus*, word bespreek. Uit die broei eksperimente het dit geblyk dat rooikleurige ouers 'n 100% rooi nageslag lewer, terwyl die kruising daarvan met normale kleur individue, 'n silwerkleurige nageslag tot gevolg gehad het. Onderteling van laasgenoemde nageslag het 'n mengsel van slegs rooi, rooi-normale kleur en normale kleur individue opgelewer. Dit blyk duidelik dat die rooi kleur nie oorge-erf word as synde die resultaat van 'n enkele resessiewe geen nie. Dit is ook nie 'n geval van albinisme nie. Dit is meer waarskynlik die resultaat van poligeniese oorerwing waarby verskeie strukturele gene en ten minste een regulatoriese geen betrokke is. Die feit dat hierdie mutant slegs 'n rooi nageslag oplewer maak dit vanuit 'n natuurbewaringsoogpunt, 'n handige plaasvervanger vir die rooi tilapia hibried.

INTRODUCTION

This study deals with permanent colour differences which are the result of genetic polymorphism (polyploidy or polychromatism) or permanent colour differences which are the result of rare mutations. Exploitation of this genetic polymorphism and rare mutants in general, has led to the production of many different strains of a particular species. This is very much the situation in the aquarium trade and species such as *Carassius auratus*, the common goldfish, are now available in more than 120 different strains (Paworth 1984) — admittedly not all of which are colour varieties.

Genetic polymorphism, or more specifically, polychromatism, is also a relatively common phenomenon in the Cichlidae. Studies done by Fryer and Iles (1972) and Ribbink *et al.* (1983) on natural populations, indicate the important role of genetic polymorphism when considering the taxonomy and identification of species from several genera of the Cichlidae.

Different colour morphs are also present in the genera *Tilapia* and *Oreochromis*, i.e. typically coloured individuals — that is the ones that display the colour that characterises the species, as well as a red-orange strain.

The interest in this red coloured *Oreochromis* is due to the several advantages it holds for aquaculture and was therefore selected for by fish culturists. The red mutant with its bright red colour and absence of black colour on the peritonium is highly preferred by consumers in several countries because it resembles the very popular seabream, *Chrysophrys major* (Safriel & Bruton 1984). It is even reputed to have a better taste than the normally coloured fish (Trewavas 1983). It is this red mutant that was used to produce the now well

known red tilapia — a hybrid which was obtained from crossing a red mutant of *O. mossambicus* and *O. niloticus* (Liao & Chen 1983). None of the red tilapia strains cultured in Taiwan and the Philippines, however, produce an all-red progeny. The Philippine strains is claimed to produce 70% red progeny and the Taiwanese strain less consistent results (Safriel & Bruton 1984). Introduction of this hybrid into South African waters may pose a serious threat to conservation.

The uncontrolled distribution of several *Oreochromis* species together with the similarities among these species as well as their capacity to interbreed, has led to widespread contamination of some of the wild and cultured stocks (Lowe-McConnell 1982). Thus, instead of introducing an alien species, it seems sensible to use an indigenous species which will rule out any problems regarding the contamination of breeding stocks and will also enhance the chances of conserving the genetic purity of the indigenous species. It was therefore decided to investigate the inheritance of the red colour in *O. mossambicus*, a species indigenous to southern Africa to see whether a suitable strain can be established.

MATERIALS AND METHODS

Experimental Stocks

Five breeding families of 4 females and 1 male of the red mutant of *O. mossambicus* were selected. The fish weighed between 32 and 40 g and were kept in 400 l aquaria. The aquaria were supplied with internal biological gravel filters. Every second week the aquaria were cleaned and 30% of the water replaced. The water was continuously aerated and heated by means of thermostatically controlled, immersion heaters. Water temperature was maintained at $28^{\circ} \pm 1^{\circ} \text{C}$. The

fish were fed commercial fish pellets as a maintenance diet at 1–2% of body mass per day. The aquaria were checked daily for nesting behaviour, spawning and mouthbrooding. The fertilized eggs were taken from the females, and hatched in breeding funnels connected to a recirculating system in which the water temperature was also maintained at $28^{\circ} \pm 1^{\circ}\text{C}$. After hatching the fry were transferred to 200 l aquaria which were maintained in the same manner. At this stage the fish were fed with ground commercial fish pellets. When the fingerlings reached a mean mass of 10–25 g they were put into plastic pools, 1.0 m deep and 3.5 m in diameter. The pools were supplied with a continuous flow of air and the water quality was maintained through a recirculating biological filter.

After four months the fish were collected from the plastic pools and breeding families (five consisting of five red mutant females and two typically coloured males each and five families consisting of five typically coloured females and two red mutant males each) were established in 400 l aquaria. The typically coloured *O. mossambicus* were recruited from stocks that were collected in Roodeplaas Dam near Pretoria, Transvaal. The aquaria were maintained in the same manner as for the previous families. The offspring obtained were also transferred to plastic pools and after four months another set of five breeding families were put together from this red mutant and typically coloured crosses. As before, each breeding family consisted of five females and two males. The offspring of this cross were treated in the same manner as in the previous experiments.

Before transfer of the offspring to the pools, all fish were inspected individually, counted and their colour noted.

RESULTS AND DISCUSSION

From the results (Table 1) it is obvious that the red mutant of *O. mossambicus* breeds true red. This immediately distinguishes this strain from the red tilapia hybrid which does not produce 100% all red progeny. Thus anything other than all red offspring will indicate contamination of the breeding stock.

It can further be seen from the results that the inheritance of the red colour does not seem to follow a simple Mendelian pattern. Before considering the possible underlying genetic mechanism, it might be helpful to refer very briefly to the manner in which colours are produced in fish. The skin contains cells called chromatophores. These may be divided into melanophores, xanthophores and erythrophores. Normally the melanin produced by the melanophores dominates whence in the absence of melanin, the red and yellow colours produced by the erythrophore and xanthophores will be detected. Thus, the colours seen in an individual fish depend to a large extent on the numbers and the degree of expansion of the different types of chromatophores. Colours are also produced by reflecting cells called iridiocytes which contain guanin

(Fryer & Iles 1972). The colour differences in *O. mossambicus* seem to originate in the chromatophores (McAndrew pers. comm.)

Let us now then consider the different possibilities of inheritance of this red colour. Dzwillo (1962) remarked that colour variants are normally the result of single recessive alleles. Such a situation is found in the so-called blue carp where the blue colour is inherited as a simple recessive trait (Probst 1949; Moav & Wohlfarth 1968). From this single gene situation it is obvious that only the homozygous recessive genotype would produce the trait. The fact that in breeding programmes with red tilapia, normal colour progeny were also obtained, rules out this possibility, although experiments with pure *O. mossambicus* mutants produced all red progeny. However, according to the results (Table 1) crossing the typical colour with the red mutant gave an F1 progeny more silvery in colour (less melanin). Interbreeding this F1 progeny produced quite unexpected results (Table 1). Out of a total of 1 172 fish, 839 displayed silvery to normal colour, 241 the red colour and then 92 displayed the red colour with 7–9 dark vertical bands. This gives a ratio of 9.1:2.6:1 which does not fit the expected Mendelian ratio of 3:1 for a recessive allele at a single locus. It is therefore obvious that the red mutant in *O. mossambicus* is not inherited as a simple recessive trait.

The second possibility considered was that of incomplete dominance as is the case in the four o'clock plant where in the heterozygous state an intermediate phenotype is produced (Dustman 1971). The intermediate silvery colour obtained in the F1 progeny after crossing a normal *O. mossambicus* with a red mutant suggested that this option warranted consideration. However, the results obtained interbreeding the F1 population indicate that there is more to it than just incomplete dominance.

The inheritance of colour proves to be complicated and seems to be controlled by several genes – that is a multiple gene interaction. We may find a situation of collaboration where two or more genes interact to produce single character phenotypes that neither gene could produce alone, e.g. the combs in chickens (Crow 1983; Dustman 1971). Another option is allelic gene interaction through epistasis. This refers to genic interactions whereby one gene may or may not be expressed because of the presence of another gene, e.g. in mice; the gene coding for melanin (A-melanin; a-albino) and colour (B-agouti; b-intense uniform colour). "A" must be present otherwise neither B nor b will be expressed (Dustman 1971). Judging from the results (Table 2) it seems that epistasis may indeed be involved in the distribution and intensity of expression of the red colour as such. The recessive homozygous state (dd) of the epistatic gene would have no effect and the normal colour would be produced. The heterozygous state of the epistatic gene (Dd) would only lead to a partial inhibition of melanin production and melanophore development and distribution producing the silvery

colour or even red/black combinations, while the dominant homozygous state (DD) of the epistatic gene would have a very high inhibitory effect on melanin formation and melanophore development and therefore result in an all red specimen.

Against this background the following explanation is proposed: The presence and density of chromatophores in the skin is coded for by at least two pairs of alleles which are incompletely dominant. Epistasis is involved in the occurrence of albinism and in the distribution and intensity of expression of chromatophores, but not in the expression of the red color as such.

Several genes, which are incompletely dominant, code for the density of chromatophores. Fish without or with few chromatophores in the skin are red. Alleles that code for the absence of chromatophores are very rare in natural populations because of selection against silvery or red individuals (apparently through predation). Let us assume that alleles A and B code for the presence of chromatophores and alleles a and b code for the absence of chromatophores (more than two loci could be involved). Alleles a and b were probably absent in the experimental group of normal coloured fish (outcome of F1). The red individuals used in the trials probably all had the genotype aabb (because they bred true). If this was so, all the F1 individuals (silvery) were AaBb. The theoretical outcome of the F1 × F1 will depend on whether the two

loci involved are situated on the same or on different chromosomes (occurrence or not of crossing over) and the distance between the loci (frequency of crossing over). In all the trials, except trial no. 3, approximately 20% of the offspring were red. This is more than the expected frequency of aabb, and if the reasoning is correct, some of the individuals identified as "red", must have had the genotype Aabb of aaBb. Further crosses with the F2 "red" individuals will show whether this is the case. The fact that the Taiwanese red tilapia does not breed true for red colour (which must be determined by the same genes: developed from "red" *O. mossambicus*), substantiates the hypothesis that red individuals are not homozygous. This is furthermore supported by the fact that red coloured individuals do vary in their amount of redness.

To conclude – the red colour in *O. mossambicus* seems to be coded through multiple gene interaction, involving several structural genes and at least one regulatory gene. Parents producing the all-red progeny, much sort after in aquaculture can, however, be achieved through careful selection programmes. Thus working with the indigenous *O. mossambicus* rules out the possibility of genetic contamination. Furthermore, red mutants that are by accident released into natural waterbodies would find it difficult to become established as a separate strain due to this intricate multiple gene interaction. Fishelson (pers. comm.) has further

TABLE 1: The number and colour of the offspring obtained in the different breeding experiments.

Pure red mutant breeding families					
Breeding families	1	2	3	4	5
No. of offspring	152	143	157	193	211
Colour of offspring	True red	True red	True red	True red	True red

Cross between red mutant and typically coloured males					
Breeding families	1	2	3	4	5
No. of offspring	193	308	267	217	245
Colour of offspring	Silvery	Silvery	Silvery	Silvery	Silvery

Cross between red mutant males and typically coloured females					
Breeding families	1	2	3	4	5
No. of offspring	231	219	287	185	226
Colour of offspring	Silvery	Silvery	Silvery	Silvery	Silvery

TABLE 2: The offspring obtained by interbreeding of the red mutant and the typically coloured cross

Breeding families	1	2	3	4	5
Total No. of offspring	167	341	172	239	253
No. according to colour	122 31 14	252 70 19	108 42 22	168 47 24	189 51 13
Colour of offspring*	B/S R B/R	B/S R B/R	B/S R B/R	B/S R B/R	B/S R B/R
Ratio of different types	8,71 : 2,21 : 1,00	13,27 : 3,69 : 1,00	4,91 : 1,91 : 1,00	7,29 : 1,97 : 1,00	14,53 : 3,92 : 1,00

* B/S = Black (normal) to Silvery
 R = Red
 B/R = Red with 7-9 black vertical bars

found that whenever red mutants are kept with typically coloured fish, they are extremely susceptible to cannibalism and also predation by birds.

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Summer activity patterns of the riparian desert beetle *Physadesmia globosa*

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ABSTRACT

The summertime activity pattern of the tenebrionid beetle *Physadesmia globosa* was investigated using focal animal sampling. Beetles have a bimodal activity pattern with activity peaks during the morning and the late afternoon. The morning activity peak is divided into an early bout of foraging, followed by sexual behaviour. There was no clear correlation between ambient temperature and daily levels of inactivity: some of the highest activity levels were recorded during the time period 16h00–17h00, when the ambient temperature was the highest. These data are discussed in the light of evolutionary explanations for beetle activity patterns.

INTRODUCTION

A significant amount of the diversity of the Namib desert fauna comprises Coleoptera (Koch 1962). The tenebrionid tribe Adesminii, including the genera *Onymacris*, *Physadesmia* and others, is prominent among these (Wharton & Seely 1982). *Physadesmia globosa* is often abundant in mixed *Acacia* spp. riparian woodland in river beds such as those of the Kuiseb and Swakop Rivers in the coastal zone of the Namib Desert (Penrith 1979; Wharton & Seely 1982). Although a number of behavioural studies have recently investigated this species (Hamilton & Penrith 1977; Nicolson *et al.* 1984; Rasmussen *et al.* 1985; Osberg & Hanrahan 1986), relatively little is still known about its behaviour.

This paper investigates the diurnal activity of *Physadesmia globosa* in greater detail than as been done before. The concept of 'activity' is ill-defined (Ferguson *et al.* 1988), because a single, quantitative measure corresponding to 'activity' does not exist. For this reason, counts of various tenebrionid beetle species carried out while doing standard transects (Hamilton 1971; 1975; Louw & Hamilton 1972; Hamilton *et al.* 1976; Wharton 1980) bias data towards beetles that are walking and that are in exposed places at the time of the count. The activity of *Physadesmia globosa* has also been recorded in terms of walking behaviour of beetles (Marden 1987) and also leads to biased data since animals can be active even though they do not move about. Feeding and mating are important activities of these beetles and often do not involve their walking about. Focal animal sampling (Altmann 1974) is a method that yields more reliable data, and information on the circadian frequency of all the important behaviour categories can be obtained.

The aim of this paper is to describe the activity patterns of *Physadesmia globosa* in terms of the important behaviour categories of this species. These data form the basis of a more detailed behavioural study in progress.

METHODS

This study was performed during February/March 1987 at Gobabeb in the central Namib Desert, SWA/Namibia. Results reported on here were obtained in an area of about 400 m², containing two large *Acacia erioloba* trees and a *Salvadora persica* thicket in the Kuiseb River bed. Behavioural data on free-ranging beetles were collected through focal animal observations (Altmann 1974). Information

from 211 observation-hours (males: 106 obs-h; females 105 obs-h) was collected, with focal periods of 1 h/individual, covering the diurnal period 08h00 to 19h00. In order to enable identification of the focal animal during the focal period and to avoid duplicating observations on any individual during the study period, each individual was given a distinctive mark by painting a small pattern on its back using white nail polish. The distance over which focal individuals moved during each observation period was measured, as was the behaviour during instantaneous scans every 60 seconds.

Climatic data were measured with a thermohygrograph in a Stevenson screen at the study site, situated on the ground underneath an *Acacia erioloba* tree where it was exposed to the sun after about 11h00. This location was representative of where beetle activity occurred throughout the day.

Because of the nonparametric nature of the information, distance data were transformed through the transformation: $d' = \ln [\text{distance (cm)} + 1]$ (Sokal & Rohlf 1981:419). Proportions of observations comprising each behavioural category during a particular diurnal hour interval (p) were transformed as: $p' = \log_{10} [\arcsin(p)]$ (Sokal & Rohlf 1981:427). Parametric tests were performed on the transformed data.

RESULTS

Five behavioural categories were observed during the study period. These were feeding, walking, chasing, buried and inactive (surface). Table 1 gives the overall proportions of time spent in each behavioural

TABLE 1: Mean amount of time *Physadesmia globosa* spent in various behavioural categories at Gobabeb during February/March 1987. (Sample size = 211, each measurement representing 1 obs-h.).

Behavioural Category	Mean percentage of time spent in this behaviour	Standard error of mean
Inactive: standing still	17 %	1.4 %
Feeding	6 %	0.6 %
Walking	30 %	1.6 %
Dug in: buried under detritus	28 %	2.3 %
Chasing (Premating & matting)	19 %	1.8 %

category. During the day the greatest amount of time (30 %) was spent walking, while just less than 30 % of the time was spent buried underneath detritus or sand. Beetles were inactive (standing still above ground) for 17 % of the day.

The level of activity before 08h00 was low: beetles were buried or inactive 75 % of the time between 08h00–09h00. None of the focal animals were active before 08h00 and individuals were difficult to find at this time. Likewise, the level of activity was low after 19h00: beetles were inactive or buried for 15 % of the time between 18h00–19h00 and none of the focal animals were active after 19h00. It therefore appears that *Physadesmia globosa* was active mainly between 08h00 and 19h00 during the study period.

The mean amounts of time spent in the five behavioural categories for each hourly interval between 08h00 and 19h00 are shown in Figure 1. A clearly bimodal activity pattern is evident for feeding, walking and chasing. The asterisks in Figure 1, resulting from multiple comparisons using Tukey's studentized range tests (Sokal & Rohlf 1981: 245), indicate mean hourly activity levels differing significantly from some other hourly values ($p < 0.05$). Instead of presenting an 11×11 matrix of Tukey's statistics for each graph in Figure 1, the results are summarised on the diagram. Thus, for chasing, data at 17h00 and 13h00 differ significantly from some other data, in this case those at 08h00 and 09h00. The text clarifies some of these differences.

Distance walked: The mean distance that beetles moved over the focal period of 1 h varied from 11.6 cm during 08h00–09h00, to 236 cm during 17h00–18h00. This parameter showed three diurnal peaks: 09h00–10h00, 13h00–14h00, and 16h00–18h00 (Figure 1B). Around 15h00 the beetles walked short distances (80 cm/h): multiple comparisons suggested, however, that distances moved during this period did not differ statistically from that of the late afternoon, but did differ from distances moved during the morning. Data from 08h00 differed significantly from those of most other hourly periods.

Walking: The amount of time spent walking around while not involved in feeding or overt sexual behaviour showed a pattern similar to that of distances moved. An early morning activity peak was, however, more

evident (Figure 1A). An increased amount of time spent walking in the late afternoon did not differ statistically from low levels of walking during midday (Tukey's multiple comparison).

Chasing: This behavioural category comprised sexual behaviour including mate following, mate guarding, mounting and attempted copulation. Like feeding, chasing showed two peaks; from 11h00–13h00 and at 17h00 (Figure 1C). Mating was less common from 14h00–15h00: however, the level of chasing at mid-day did not differ statistically from those at other times of day (Tukey's multiple comparison).

Digging in (buried): Beetles often buried themselves at night, as well as during the day between 12h00–15h00 (Figure 1D). The cover used during this period normally consisted of detritus (dead *Acacia* leaflets) or other vegetation. The amount of time spent buried during midday differed statistically from those during early morning and late afternoon (multiple comparison).

Periods of inactivity: Beetles were inactive (i.e. standing still) early in the morning before 09h00 and in the afternoon, the amount of time spent inactive increasing after 14h00 (Tukey $p < 0.05$; Figure 1D). Levels of inactivity did not resemble those for digging in and showed a small peak during the period of decreased chasing, feeding and walking around 15h00. Levels of inactivity at this time did not differ statistically from those at mid-day (multiple comparison).

Feeding: Feeding was the most commonly recorded activity between 09h00 and 11h00 (Figure 1E). A second, but less important, peak in feeding occurred from 16h00–17h00, with a period of low feeding activity during 13h00–15h00. However, Tukey's multiple comparison suggested that the afternoon peak in feeding did not differ statistically from feeding levels at other times of day.

Ambient temperature: At 08h00 the ambient temperature was about 13°C, while the hottest part of day was between 15h00 and 18h00, when the mean ambient temperature exceeded 28°C (Figure 1F).

DISCUSSION

A bimodal activity pattern has been suggested for the Namib tenebrionids *Lepidochora discoidalis* (Louw & Hamilton 1972), *Onymacris plana* (Henwood 1975), *Onymacris rugatipennis* (Hamilton *et al.* 1976), three species of Zophosini (Wharton 1980) and for *Onymacris langi* and *Physadesmia globosa* (Hamilton 1975). Both Hamilton (1975) and Wharton (1980) remarked that the activity of tenebrionids appeared to be unimodal during cool days when exposure to the sun and overheating is reduced. The present observations were made during the hottest time of the year at Gobabeb (Weather Bureau 1985): observations during winter are likely to show trends similar to those observed by these authors.

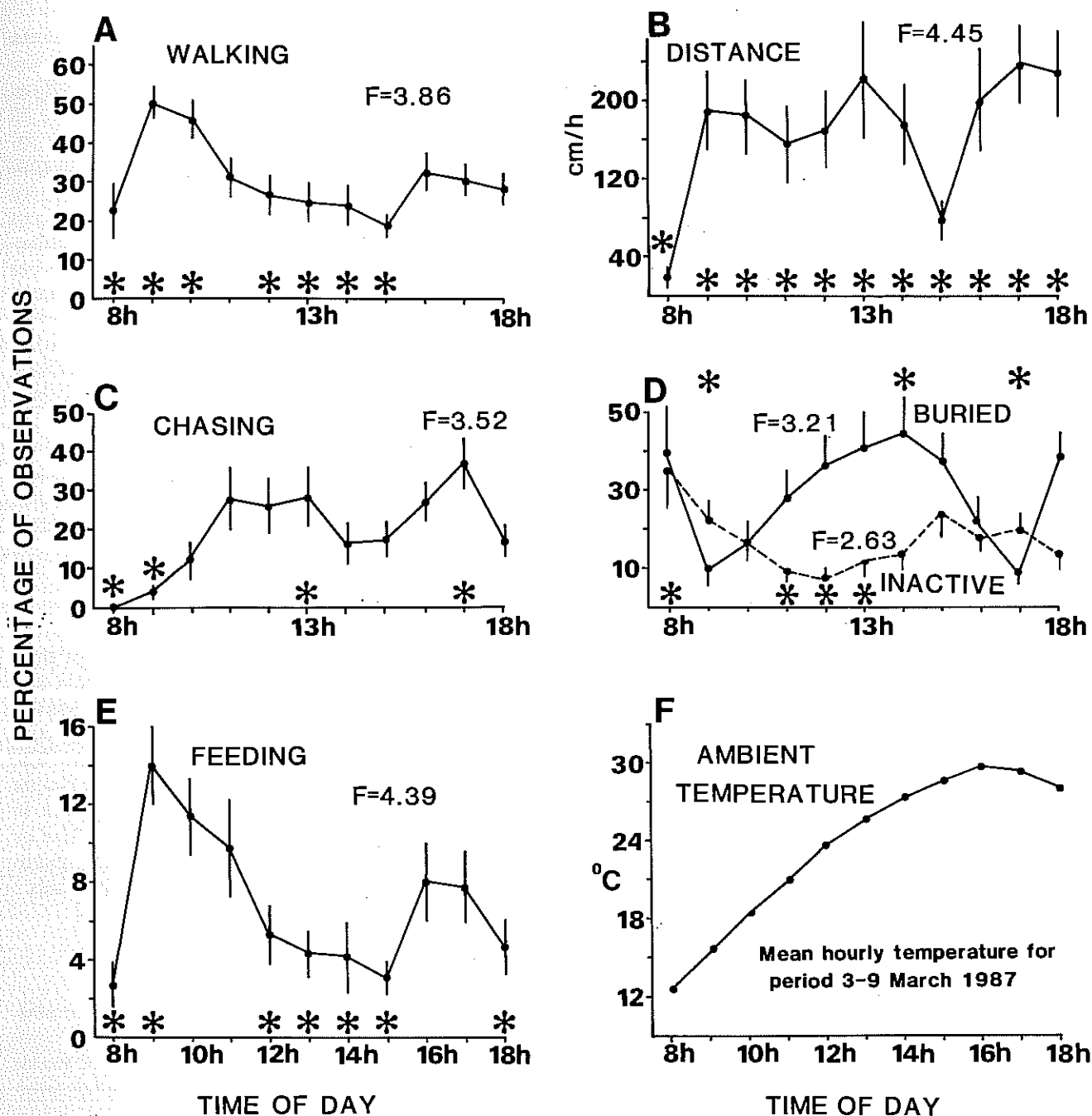


FIGURE 1. Mean percentages of time that *Physadesmia globosa* spent in various behavioural categories at different times of the day during February and March 1987. Tick marks indicate hourly periods starting with the indicated time, e.g. 18 h represents the hour 18h00–19h00. F-values (d.f. = 10, 189) resulting from a single classification ANOVA on transformed data indicate the significance ($p < 0.005$ in all cases) of diurnal variations in behavioural patterns over the 11 hourly periods. Asterisks indicate mean hourly activity levels differing significantly from other hourly values of the same behavioural category (Tukey's studentised range test, $p < 0.05$). Vertical bars indicate SEM. Figure 1D indicates variations in amount of time inactive aboveground (broken line; bottom F-value and asterisks) and time buried (solid line; top F-value and asterisks).

If therefore appears that the crude activity measures used on *P. globosa* by Hamilton (1975) and Marden (1987) do in fact reflect the walking, feeding and mating behaviour of this species.

This study revealed that the morning activity peak is clearly divided into two components: feeding takes place mostly before 11h00 (Figure 1E) while chasing behaviour is performed mostly after 11h00 (Figure 1C). These two peaks are reflected in Figure 1B which depicts the activity as measured in terms of distance

walked per hourly observation period. One would expect that two factors, the relatively cool temperatures of the morning before 11h00 (Figure 1F) and the fact that feeding behaviour does not require walking over large distances would predispose beetles towards shorter distances moved before 11h00. Figure 1A, however, indicates that *P. globosa* individuals move over large distances soon after becoming active after 09h00. In addition, beetles spent a significantly greater amount of time (Tukey multiple comparison $p < 0.05$; Figure 1A) walking during the early feeding

peak (around 09h00) than during the late morning (around 12h00) when chasing behaviour was more prevalent. Although not statistically different, *P. globosa* appears to spend more time feeding during the morning than during the afternoon: the morning peak is 3 h long and higher than the 2 h long feeding peak around 17h00. This phenomenon is not surprising as one would expect these small animals to be in need of food immediately after a period of inactivity lasting about 12 h overnight.

Mean relative humidity often came close to the saturation point in the early mornings between 06h00 and 08h00. This would cause the moisture content of the detritus upon which the beetles feed to be greater before 10h00 than at other times of the day and could be an important source of moisture in a desert environment. If this were the case, early morning feeding would be advantageous.

Chasing behaviour included mate following, mate guarding, mounting and attempted copulation: all these components of mating behaviour showed a bimodal pattern broadly resembling the behavioural categories discussed above. The spurt of chasing activity in the late afternoon (around 17h00) was the highest of the day (Figure 1C).

P. globosa individuals often dig themselves into detritus or sand of the Kuiseb River bed in a similar way to other Adesmiini, e.g. *Onymacris unguicularis* in the sand dunes (Louw *et al.* 1986). *P. globosa* individuals spent the least amount of time buried beneath sand during the early morning feeding period (around 09h00) and during the late afternoon (around 17h00). Digging could, however not be directly correlated with the daily temperature (Figure 1F) or humidity profiles at the study site: the highest temperatures and the lowest humidities normally occurred after 15h00, when the amount of time spent beneath the sand was decreasing rapidly (Figure 1D).

Above-ground inactivity was the most prevalent during the early morning and during the afternoon from 14h00–17h00, when chasing, feeding and walking were at low levels. This behavioural category invariably occurred in the dappled shade of *Acacia erioloba* trees or *Salvadora persica* thickets. The early morning period of inactivity was associated with the emergence of beetles from their nocturnal sleeping places. It therefore appears that surface inactivity is not directly connected with digging behaviour.

From an evolutionary point of view, a bimodal activity pattern need not be an evolved adaptation in response to an environmental constraint, but could be a fortuitous effect. As far as feeding is concerned, one would expect a high feeding level immediately after an animal has become active. If a large part of the animal's food requirements were met by early feeding, a later drop in feeding would be the fortuitous effect of sufficient food intake. In the case of *P. globosa*, however, all the behavioural categories show a bimo-

dal pattern, including chasing and time buried. As the latter two behavioural patterns are probably not governed by the same motivational factors as feeding, it is unusual to find a bimodal activity pattern in all these behavioural categories. This is not easily explainable as an effect and one should therefore consider the possibility that the bimodal activity pattern is an evolved adaptation. However, this paper does not offer data providing the adaptiveness of a bimodal activity pattern. In the literature, much discussion has surrounded this type of activity pattern of Namib tenebrionid beetles: Hamilton (1975) used bimodal data in support of his maxithermy hypothesis while Henwood (1975) and Wharton (1980) emphasised that this activity pattern is advantageous because of heat stress avoidance. Hamilton, however, subsumes the latter explanation in his hypothesis. The heat stress hypothesis is relatively easily and directly testable and because of its simplicity, should have preference over higher-level hypotheses like the maxithermy hypothesis.

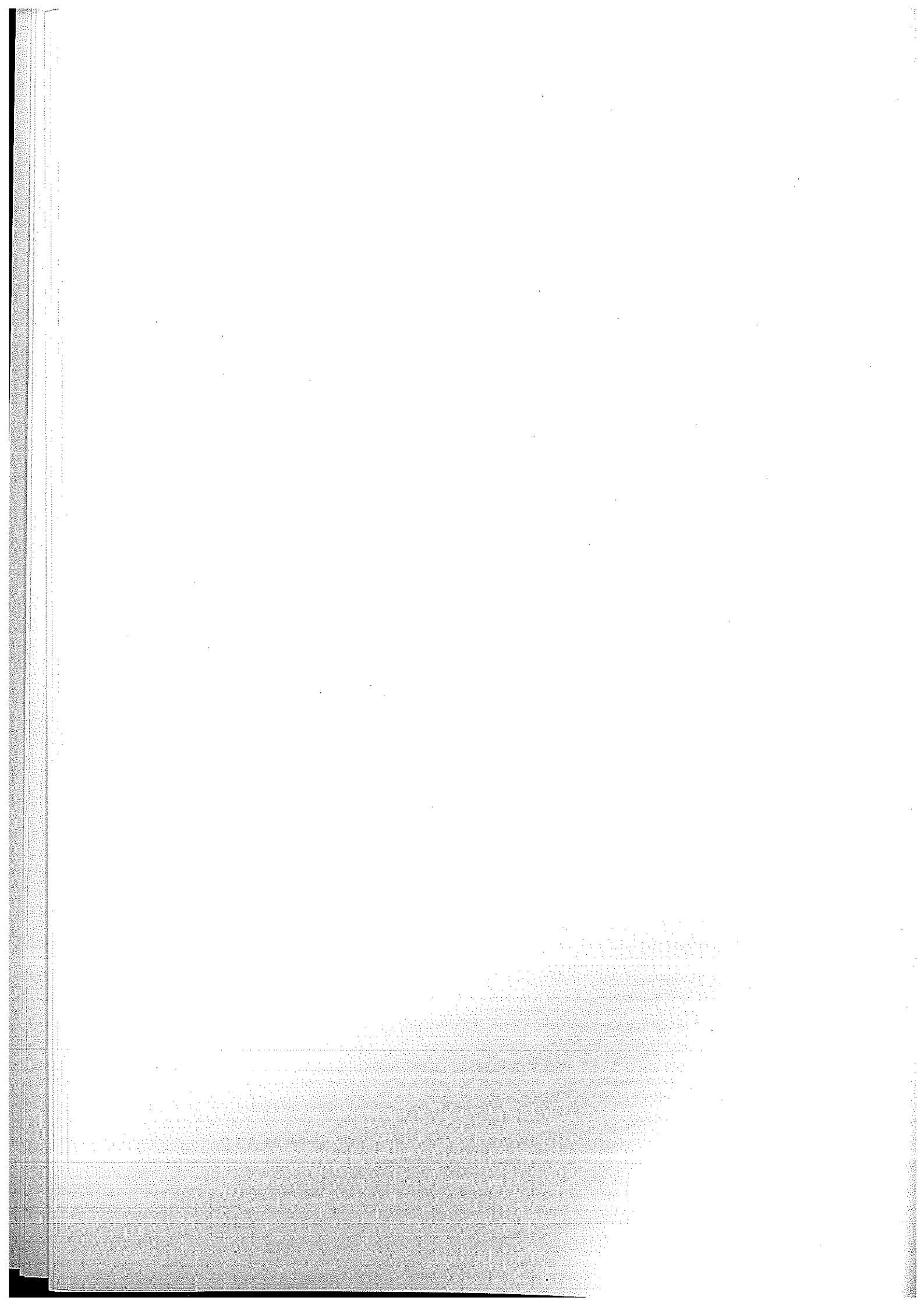
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Veld dynamics and utilisation of vegetation by herbivores on the Ganias Flats, Skeleton Coast Park, SWA/Namibia

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ABSTRACT

Veld surveys and game counts were conducted quarterly during 1982 and seasonally during 1983/84 on a typical pro-Namib plain on the eastern boundary of the Skeleton Coast Park. A strong correlation between veld condition and rainfall was evident. The perennial vegetation of the river washes remained greener than the annual grasses on the gravel plains. Most game migrated eastwards during the rainy season in response to improved inland pastures, brought about by the east-west rainfall gradient of the Namib Desert. Game returned to the study site during the drier months, utilising chiefly the vegetation of the river washes. Very low game numbers were recorded and herbivores utilised only a small fraction of the available and apparently suitable forage.

INTRODUCTION

The aim of this study was to establish the relationship between fluctuations in veld conditions and the seasonal movements of large herbivores on a typical pro-Namib plain along the eastern boundary of the Skeleton Coast Park.

The climate of the Namib Desert is characterised by low average temperatures, high humidity and the presence of fog with an increase in temperature and a decrease in humidity eastwards from the coast (Seely 1978a). Rain is regarded as the single most important factor in desert and semi-desert ecosystems (Seely & Stuart 1976; Viljoen 1980), and a direct correlation between rainfall and vegetation cover has been observed in both the central Namib (Seely 1978b; Nel *et al.* 1985) and in Kaokoland (Viljoen 1980).

After good rains fell in the northern Namib Desert and western Kaokoland during March–April 1982, the vegetation cover on the pro-Namib plains changed dramatically, providing an ideal habitat for herbivores, birds and insects. Previous ground-based game counts and aerial surveys indicate that game densities on these plains show noticeable seasonal and annual fluctuations (Viljoen 1980, 1982a, 1982b; Skeleton Coast Park unpublished data). At present the boundaries of the Skeleton Coast Park are unfenced and no pastoral or game management is practised in this area.

SITE DESCRIPTION

The study site, situated on the Ganias Flats, was 55 km long and 5 km wide. This area lies between the Hoanib and Hoarusib Rivers and is bisected by the eastern boundary of the Skeleton Coast Park (Figure 1). To the west of the Ganias Flats lie the sand dunes of the northern Namib Desert and to the east, plains extend until the mountainous regions of the Kaokoland escarpment. The study site falls within the western part of the pro-Namib and is characterised by sparsely vegetated plains and numerous river washes. Although rain may be absent for several years, the area receives an average rainfall of 30–100 mm per annum (Viljoen 1980). The Aridosols of the plains are described as be-

ing mostly unconsolidated and comprised chiefly of stone, gravel and fine sand while the Entisols of the river washes, where a measure of soil differentiation occurs, have a higher degree of organic material (Viljoen 1980).

METHODS

Two habitat types, namely gravel plains and river washes, were recognised. These habitats were surveyed

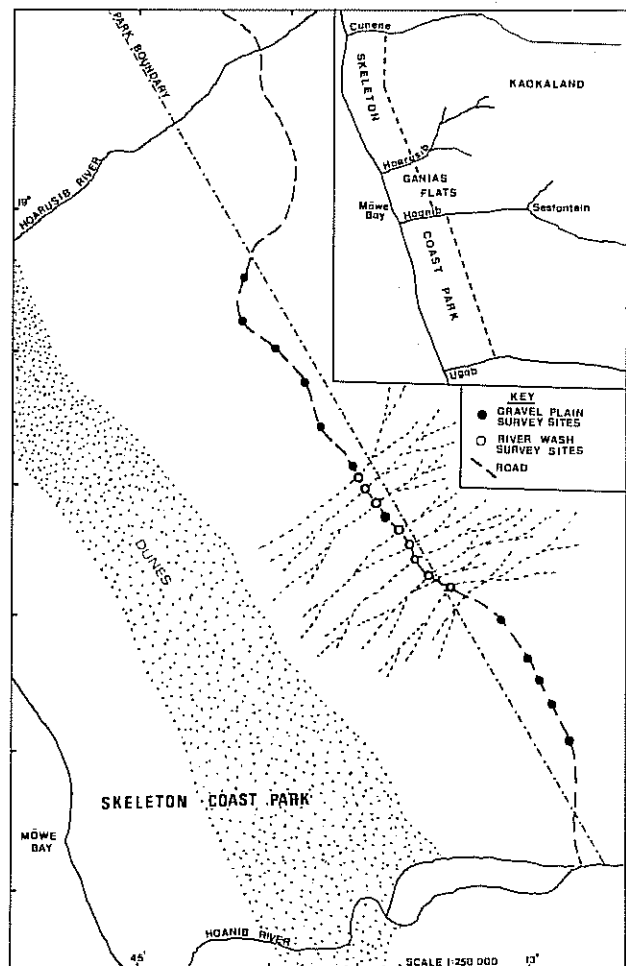


FIGURE 1: The Ganias flats showing gravel plain and river wash survey sites.

separately using the step point method, a modification of the wheelpoint method described by Tidmarsh and Havenga (1955).

Twelve sites on the gravel plains, approximately 3 km apart, and eight river washes, were surveyed on a quarterly basis during 1982, and on a seasonal basis during 1983 and 1984. Three seasons were recognised as follows: a wet season (January–April), a cool dry season (May–August) and a hot dry season (September–December).

At each site, a metal rod (diameter 5 mm) was plunged vertically into the ground every 2 m. For each plunge the following information was recorded during the 1982 surveys:

1. the plant species nearest to the rod, and
2. in the case of a strike, whether or not it was a basal hit.

During the seasonal surveys of 1983–84 the following information was recorded for each plunge:

1. the plant species nearest to the rod,
2. in the case of a strike whether it was a crown or basal hit,
3. the estimated percentage green material of that plant, and
4. the estimated percentage utilisation of that plant by mammalian herbivores and insects.

A total of 2 448 points for the gravel plains and 2 128 points for the river washes were recorded during each survey.

Seasonal ground-based game counts were conducted along the main route through the study area and attempts were made to record direct utilisation of plants by herbivores. As rain gauges erected on the Ganias flats were repeatedly knocked over and destroyed by hyaenas, rainfall data were obtained from the weather stations at Möwe Bay and Sesfontein. (Figure 1).

The following formulae were used to obtain the values mentioned in the Tables and Figures.

- The Index of Greenness (I_G) for species x

$$= I \times A$$
 where I = percentage green material of species x
 $\div 100$
 A = the relative abundance of species x .
- The Index of utilisation of species x

$$(IU) = U \times A$$
 where U = percentage utilisation of species x
 $\div 100$
 A = relative abundance of species x .
- The Palatability Factor (B) of species $x = \frac{E \times U}{S}$
 where U = percentage of utilisation of species x
 $\div 100$
 S = the total number of species \times scored
 E = the number of species \times showing signs of herbivore utilisation.
- The Attractance Value (AV) of species $x = B \times I$.

RESULTS

Rainfall data from Möwe Bay and Sesfontein and the indices of greenness for both habitat types on the Ganias Flats are presented in Figure 2, together with game count data gathered from the study area between June 1982 and May 1984. The seasonal fluctuations in the percentage crown and percentage basal cover on the Ganias Flats during the duration of the study are depicted in Figure 3 and the indices of herbivore utilisation for the river washes and gravel plains are illustrated in Figure 4. The relative abundance and percentage basal cover of the most common plant species encountered are given in Table 1 and 2. The index of greenness, index of utilisation by mammalian herbivores and the palatability factors of plants utilised between January 1983 and May 1984 are given in Tables 3 and 4. The Attractance values of all plants utilized are summarised in Table 5. The index of utilisation of plants showing damage by insects are summarised in Table 6 and a species breakdown of game count figures is given in Table 7.

DISCUSSION

Rainfall

The difference in rainfall received at Möwe Bay and at Sesfontein during the period 1982–1984 (Figure 2),

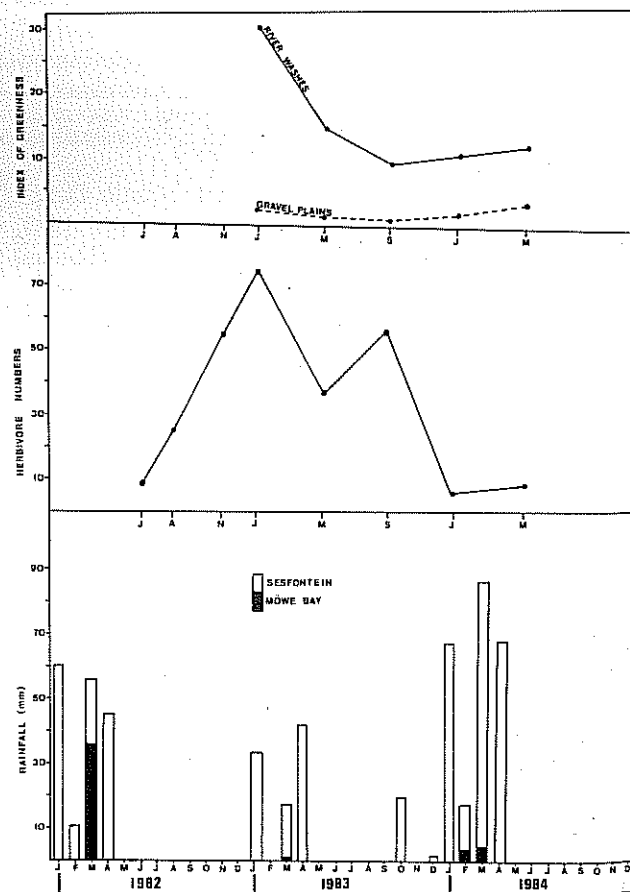


FIGURE 2: Rainfall data, fluctuating herbivore numbers and the index of greenness of vegetation on the Ganias flats.

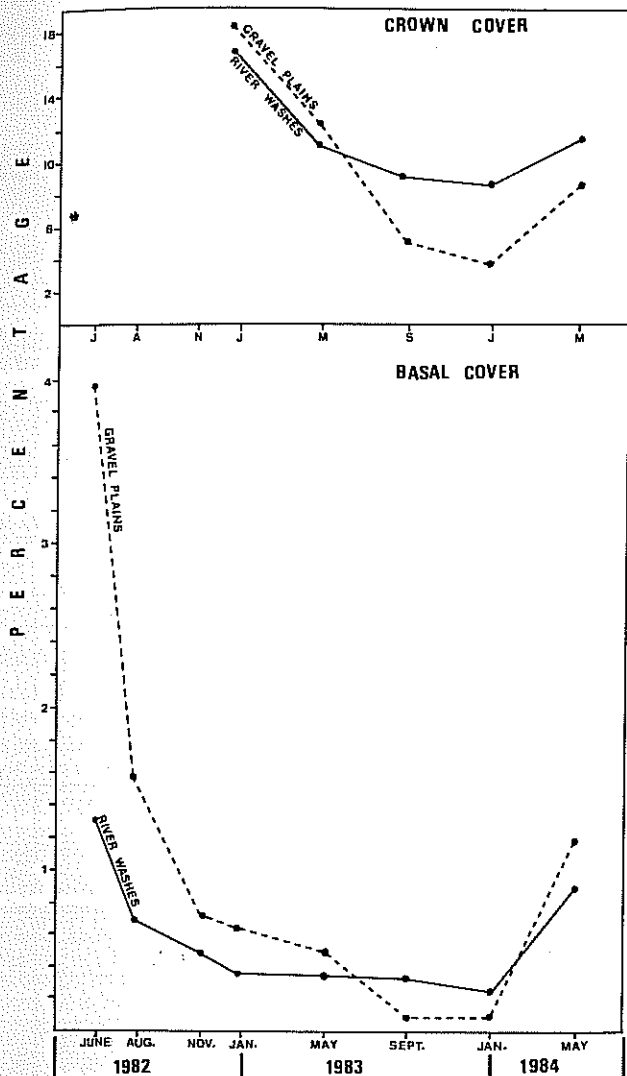


FIGURE 3: Fluctuations in the vegetation cover on the Ganiias flats between 1982 and 1984.

clearly illustrates the east-west rainfall gradient which is typical of the Namib Desert. Rainfall during this period was highly sporadic (Figure 2). In 1982 the study site and surrounding areas received the first heavy showers in years (pers. obs.). Although Sesfontein received 73,5 mm of rain during the following year, almost no rain fell at the coast and all indications suggest that <1 mm fell on the Ganiias Flats. In 1984 more substantial rains fell over the entire area with Sesfontein receiving 220,7 mm while 9 mm fell at the coast. It is therefore assumed that a minimum of 10 mm fell on the Ganiias Flats during this period.

Species composition and abundance

On the Ganiias Flats, the river washes support a far greater species diversity and a higher proportion of perennial plants than the gravel plains which are comprised mostly of ephemeral and annual grasses (Tables 1 & 2). Most species remained present during the dry period of 1983, although significant changes in individual species abundance were recorded between 1982 and 1984 (Tables 1 and 2). On the gravel plains, *S. uniplumis* var. *intermedia* and *S. hochstetterana* re-

mained dominant and co-dominant throughout the study period, while *S. hochstetterana* and *G. spinosa* remained the two most common river wash species (Tables 1 & 2).

Crown and basal cover

The vegetation cover on the Ganiias Flats varies seasonally and annually in response to environmental factors such as rainfall fluctuations and drought. The light showers which fell during March 1983 were not sufficient to bring about any change in the gradual decline in vegetation cover, which improved only after the more substantial 1984 rains (Figure 3). Using basal cover as a veld condition indicator it was evident that during the course of this study the gravel plains, with their higher proportions of annual grass species, reacted more drastically to environmental factors than did the river washes (Figure 3). During the dry months of 1983 the basal cover on the gravel plains was low to virtually non-existent in places. However, the river washes with their higher perennial component, maintained a relatively high, albeit fluctuating, vegetation cover throughout all seasons. A similar situation was noted on the central Namib plains during times of drought (Nel *et al.* 1985).

On the Ganiias Flats annuals such as *S. uniplumis* var.

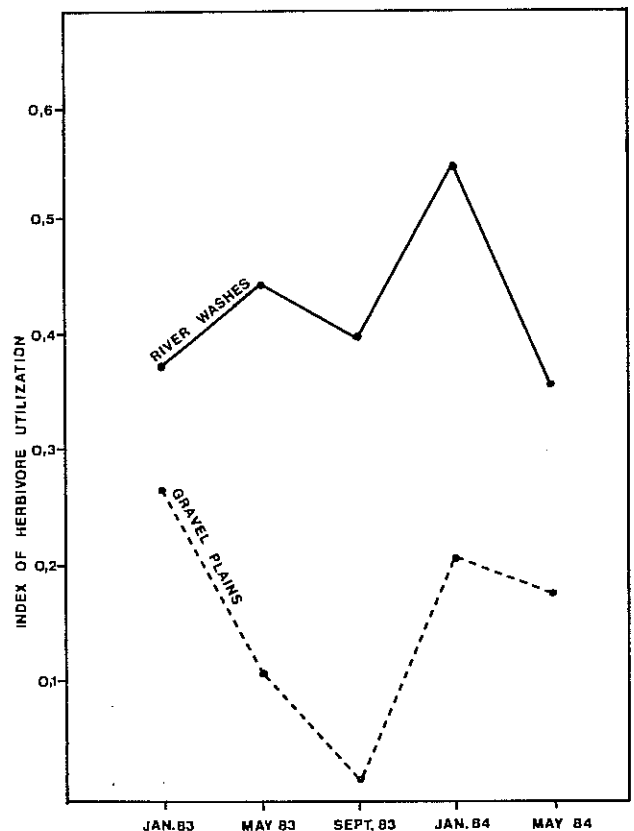


FIGURE 4: The indices of vegetation utilisation by herbivores on the gravel plains and river washes of the Ganiias flats between 1983 and 1984.

TABLE 1: The relative abundance (A) and the percentage basal cover (Bc) of the most common species encountered on the gravel plains of the Gambia Flats.

	JUNE 1982		AUG. 1982		NOV. 1982		JAN. 1983		MAY 1983		SEPT. 1983		JAN. 1984		MAY 1984	
	A	Bc	A	Bc	A	Bc	A	Bc	A	Bc	A	Bc	A	Bc	A	Bc
<i>Stipagrostis hochstetterana</i>	14,30	0,51	19,57	0,45	15,77	0,12	11,19	0,16	20,79	0,12	19,44	0,04	17,03	0,12	20,95	0,29
<i>S. uniplumis</i> var. <i>intermedia</i>	45,60	1,76	46,36	0,49	49,31	0,25	42,97		42,65	0,08	41,70		47,63		53,63	0,65
<i>S. subacutalis</i>	12,00	0,74	11,93	0,20	12,87	0,25	17,77	0,16	14,09	0,12	14,80	0,04	15,24	0,04	2,98	0,08
<i>Trianthema triquetra</i>	12,90	0,32	12,58	0,25	12,25	0,04	18,38	0,08	13,15	0,04	14,70		10,74		12,76	
<i>Lotononis platycarpus</i>	5,70	0,46	1,80		1,88		3,10	0,04	2,21		3,60		2,45		0,45	
<i>Zygophyllum simplex</i>	4,13	0,13	2,78	0,08	2,82		2,12	0,08	1,47		0,53		0,37		0,78	
<i>Sesuvium sesuvioides</i>	1,90	0,13	2,29	0,08	2,33	0,04	2,53		3,55		3,30		2,94		4,25	
<i>Kolautia lasiocarpa</i>	1,20		1,31		0,82		0,45		0,29		0,04				0,12	
<i>Tephrosia dregeana</i>	0,60		0,37		0,29		0,33		0,08		0,60		0,25		0,41	
<i>Heliotropium oliveranum</i>	0,09		0,04		0,08		0,12		0,08		0,04		0,20		0,12	
<i>Euphorbia phylloclada</i>	0,09		0,12		0,33		0,12		0,16		0,40					
<i>Helichrysum gariepium</i>			0,25		0,33		0,61		0,57		0,40		0,86		0,61	
<i>Geigeria spinosa</i>	0,05		0,20		0,29	0,04	0,12		0,16		0,66		0,65		0,45	
<i>Indigofera</i> spp.	0,23				0,12		0,08									
<i>Cleome foliosa</i>							0,04		0,20				0,45		1,02	
<i>Osteospermum microcarpum</i>															0,49	
<i>Adenolobus pectuelii</i>					0,12				0,08		0,12		0,65		0,41	
<i>Petalidium angustifolium</i>	0,05				0,29				0,04		0,16		0,53		0,41	

TABLE 2: The relative abundance (A) and the percentage basal cover (Bc) of the most common species encountered in the river washes of the Gambia Flats.

	JUNE 1982		AUG. 1982		NOV. 1982		JAN. 1983		MAY 1983		SEPT. 1983		JAN. 1984		MAY 1984	
	A	Bc	A	Bc	A	Bc	A	Bc	A	Bc	A	Bc	A	Bc	A	Bc
<i>Stipagrostis hochstetterana</i>	12,47	0,10	36,1	0,23	20,39	0,09	19,55	0,05	25,05	0,28	23,92	0,09	24,01		31,02	0,14
<i>S. uniplumis</i> var. <i>intermedia</i>	35,29	0,39	8,27	0,14	22,18	0,09	16,02		7,89		5,92		7,00		3,10	
<i>S. namaquensis</i>									1,13		0,47		0,80		2,30	
<i>Asteratherum</i> spp.			1,88		2,4	0,05	0,89		1,55	0,05	0,70		0,89		1,03	
<i>Petalidium</i> spp.			2,3		1,27	0,05	1,92		2,16		1,69	0,05	1,03		2,68	0,05
<i>P. angustifolium</i>	0,24		2,16		0,8		0,47		2,40		2,07	0,05	2,02		3,24	0,05
<i>Geigeria spinosa</i>	13,29	0,19	10,67	0,14	14,14	0,05	16,45	0,05	12,95		18,52	0,05	19,92	0,18	15,65	0,23
<i>Tephrosia dregeana</i>	2,94		6,3		7,05	0,05	9,49		6,11	0,05	5,73		4,61		3,76	0,05
<i>Merremia</i> spp.	2,6	0,14	1,08	0,05	2,02	0,05	2,26	0,05	2,54		3,05		2,82		3,57	
<i>Cleome foliosa</i>			0,05		0,61						0,23		1,27		2,44	
<i>Osteospermum microcarpum</i>	3,76		5,6		4,62		6,06	0,05	9,92		10,62	0,05	8,65		7,71	
<i>Helichrysum gariepium</i>	1,03		4,09		5,55		6,11	0,05	7,66	0,05	6,34		7,42		4,79	
<i>Kolautia lasiocarpa</i>	15,12	0,14	7,19		6,02	0,05	4,23		3,81		3,90		0,99		2,02	
<i>Heliotropium oliveranum</i>	0,29		0,8		0,23		0,23		0,09		0,09		0,09			
<i>Zygophyllum stapfii</i>	2,36	0,10	3,52	0,09	4,23		4,51	0,05	5,36		5,92	0,05	6,91	0,09	6,53	0,19
<i>Z. simplex</i>	2,31	0,10	0,28		0,66		0,14		0,05							
<i>Sesuvium sesuvioides</i>	1,25		1,27		1,32		1,23	0,05	1,03							
<i>Lebeckia</i> spp.	1,73		3,43		3,24		6,60		10,25		1,13		0,89		2,02	
<i>Lotononis platycarpus</i>	1,25	0,05	0,19		0,09		0,52		0,19		0,14		0,23		6,63	0,05
<i>Salsola</i> spp.	0,19		0,19		0,09		0,33		0,19		0,09		0,38			
<i>Trianthema triquetra</i>	1,25		0,75		0,56		0,23		0,19		0,09		0,85		0,14	
<i>Tricholeana monachne</i>							0,23		0,23		0,38		0,09			
<i>Hemsteadia</i> spp.							0,14		0,28		0,47				0,19	
<i>Euphorbia phylloclada</i>			0,61		0,52		0,70		0,33		0,33		0,23		0,09	
<i>E. damarana</i>	0,72		0,52		0,52		0,14		0,33		0,33		0,23		0,09	

	JAN. 1983			MAY 1983			SEPT. 1983			JAN. 1984			MAY 1984		
	IG	IU	B	IG	IU	B	IG	IU	B	IG	IU	B	IG	IU	B
<i>Hemisteadtia</i> spp.	0.72	0.61	0.52	0.52	0.14	0.28	0.47	0.19	0.23	0.33	0.33	0.23	0.47	0.09	0.23
<i>Euphorbia phylloclada</i>	0.72	0.52	0.32	0.05	0.70	0.23	0.14	0.23	0.23	0.14	0.23	0.23	0.14	0.23	0.23
<i>E. damarana</i>	0.72	0.52	0.32	0.05	0.70	0.23	0.14	0.23	0.23	0.14	0.23	0.23	0.14	0.23	0.23
<i>Stipagrostis hochstetterana</i>	0.8191	0.1925	5.6 × 10 ⁻⁴	0.1601	0.0894	5.1 × 10 ⁻⁵	0.0486	0.0214	2.3 × 10 ⁻⁶	0.4668	0.1238	1.2 × 10 ⁻⁵	1.7368	—	—
<i>S. uniplumis</i> var. <i>intermedia</i>	0.0283	0.0748	4.9 × 10 ⁻⁶	0.0043	—	—	—	—	—	—	—	—	2.5474	—	—
<i>S. subcaulis</i>	0.0320	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Trianthema triquetra</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lotononis platycarpus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Zygophyllum simplex</i>	1.1783	—	—	0.4921	—	—	0.0428	—	—	0.1398	—	—	0.0720	—	—
<i>Sesuvium sesuvioides</i>	0.1429	—	—	0.0185	—	—	—	—	—	—	—	—	—	—	—
<i>Kohautia lasiocarpa</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tephrosia dregeana</i>	0.1939	—	—	0.0204	—	—	0.0214	—	—	—	—	—	—	—	—
<i>Heliotropium oliverianum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Euphorbia phylloclada</i>	0.0080	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helichrysum gariepinum</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Geigeria spinosa</i>	—	—	—	0.0040	—	—	—	—	—	—	—	—	—	—	—
<i>Indigofera</i> spp.	0.0400	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cleome foliosa</i>	0.0400	—	—	0.0640	0.0280	5.6 × 10 ⁻²	—	—	—	0.1800	0.0736	5.9 × 10 ⁻²	0.4202	0.1795	7.0 × 10 ⁻²
<i>Osteospermum microcarpum</i>	—	—	—	0.0040	—	—	—	—	—	—	—	—	0.0571	—	—
<i>Adenolobus pechuelli</i>	—	—	—	0.0240	—	—	0.0100	—	—	0.0650	0.0244	2.3 × 10 ⁻³	0.0615	—	—
<i>Petalidium angustitibum</i>	—	—	—	—	—	—	0.0640	—	—	0.1957	—	—	0.0246	—	—

TABLE 4: The index of greenness (IG), index of utilization (IU), and the palatability factors (B) of utilised plants in the river washes of the Gannias Flats.

	JAN. 1983			MAY 1983			SEPT. 1983			JAN. 1984			MAY 1984		
	IG	IU	B	IG	IU	B	IG	IU	B	IG	IU	B	IG	IU	B
<i>Stipagrostis hochstetterana</i>	3.2355	0.0743	5.5 × 10 ⁻⁵	0.6087	0.1227	3.7 × 10 ⁻⁵	0.0933	0.0383	9.4 × 10 ⁻⁶	0.2641	0.0024	1.9 × 10 ⁻⁷	0.2729	0.0062	3.0 × 10 ⁻⁵
<i>S. uniplumis</i> var. <i>intermedia</i>	0.4966	—	—	—	—	—	—	—	—	—	—	—	0.0093	—	—
<i>S. namaquensis</i>	0.0855	—	—	0.2351	—	—	0.0611	0.0141	3.0 × 10 ⁻³	—	—	—	0.4831	—	—
<i>Asternatherum</i> spp.	0.3466	—	—	0.0705	—	—	0.0420	0.1260	4.8 × 10 ⁻²	—	—	—	0.1591	—	—
<i>Petalidium</i> spp.	1.3496	—	—	0.7983	—	—	—	—	—	0.0093	—	—	0.0469	—	—
<i>P. angustitibum</i>	0.3760	—	—	1.4729	—	—	—	—	—	1.0476	—	—	1.3430	—	—
<i>Geigeria sponosa</i>	6.8004	—	—	0.9509	—	—	—	—	—	0.7509	—	—	0.1127	—	—
<i>Tephrosia dregeana</i>	2.3933	0.0522	5.4 × 10 ⁻⁵	0.3287	—	—	—	—	—	0.0796	—	—	0.0094	—	—
<i>Merremia</i> spp.	1.2905	—	—	1.3054	—	—	1.0275	—	—	1.3418	0.0564	1.0 × 10 ⁻³	1.8778	—	—
<i>Cleome foliosa</i>	0.6768	0.1786	8.6 × 10 ⁻²	0.8782	0.3146	1.4 × 10 ⁻¹	0.1150	0.0230	2.0 × 10 ⁻²	0.6444	0.4652	2.6 × 10 ⁻¹	1m1956	0.3416	5.6 × 10 ⁻²
<i>Osteospermum microcarpum</i>	2.5276	—	—	0.9563	—	—	0.5639	0.2071	1.1 × 10 ⁻³	0.3034	—	—	0.0332	—	—
<i>Helichrysum gariepinum</i>	0.2322	—	—	—	—	—	0.1395	—	—	0.0890	—	—	0.0422	—	—
<i>Kohautia lasiocarpa</i>	0.6087	0.0423	2.2 × 10 ⁻⁴	0.1318	—	—	0.0468	—	—	0.0236	—	—	0.8219	—	—
<i>Heliotropium oliverianum</i>	0.0644	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Zygophyllum stapfii</i>	3.0079	—	—	4.3019	—	—	3.4389	—	—	3.6478	—	—	—	—	—
<i>Z. simplex</i>	0.1200	—	—	0.0300	—	—	—	—	—	—	—	—	—	—	—
<i>Sesuvium sesuvioides</i>	0.1561	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lebeckia</i> spp.	4.8371	—	—	3.9800	—	—	—	—	—	—	—	—	3.4739	0.0091	2.0 × 10 ⁻⁴
<i>Lotononis platycarpus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Salsola</i> spp.	0.2217	—	—	0.1330	—	—	0.0270	—	—	0.2423	—	—	—	—	—
<i>Trianthema triquetra</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tricholeana monachne</i>	0.0376	—	—	0.0920	—	—	—	—	—	—	—	—	—	—	—
<i>Hemisteadtia</i> spp.	0.0735	—	—	0.1073	—	—	0.0564	0.0188	4.0 × 10 ⁻³	—	—	—	0.1203	—	—
<i>Euphorbia phylloclada</i>	0.2707	—	—	—	—	—	0.1082	—	—	0.0736	—	—	0.0383	—	—
<i>E. damarana</i>	—	—	—	0.0552	—	—	0.0323	—	—	—	—	—	0.1794	—	—
<i>Tephrosia oxygona</i>	0.0630	0.0816	2.0 × 10 ⁻¹	—	—	—	—	—	—	—	—	—	0.0405	—	—

TABLE 5: The attractance values of utilized plants on both gravel plains (GP) and river washes (RW) on the Ganas Flats.

	JAN. 1983		MAY 1983		SEPT. 1983		JAN. 1984		MAY 1984	
	GP	RW	GP	RW	GP	RW	GP	RW	GP	RW
<i>Stipagrostis hochstetterana</i>	$4,6 \times 10^{-4}$	$1,8 \times 10^{-4}$	$8,0 \times 10^{-6}$	$2,3 \times 10^{-5}$	$1,0 \times 10^{-7}$	8×10^{-7}	$5,7 \times 10^{-6}$	$5,0 \times 10^{-7}$	—	8×10^{-7}
<i>S. uniplumis</i> var. <i>intermedia</i>	$1,0 \times 10^{-7}$	—	—	—	—	—	—	—	—	—
<i>S. namaquensis</i>	—	—	—	—	—	$1,8 \times 10^{-4}$	—	—	—	—
<i>Kohautia lasiocarpa</i>	—	$1,4 \times 10^{-4}$	—	—	—	—	—	—	—	—
<i>Tephrosia dregeana</i>	—	$1,6 \times 10^{-4}$	—	—	—	—	—	—	—	—
<i>T. oxygona</i>	—	$1,3 \times 10^{-2}$	—	—	—	—	—	—	—	—
<i>Cleome foliosa</i>	—	$5,8 \times 10^{-2}$	$3,6 \times 10^{-3}$	$1,2 \times 10^{-1}$	—	$2,3 \times 10^{-3}$	$1,1 \times 10^{-2}$	$1,6 \times 10^{-1}$	$3,0 \times 10^{-2}$	$6,8 \times 10^{-2}$
<i>Astenatherum</i> spp.	—	—	—	—	—	$2,0 \times 10^{-3}$	—	—	—	—
<i>Osteospermum microcarpum</i>	—	—	—	—	—	$6,3 \times 10^{-4}$	—	—	—	—
<i>Hermsteadtia</i> spp.	—	—	—	—	—	$2,3 \times 10^{-4}$	—	—	—	—
<i>Adenolobus pechuelli</i>	—	—	—	—	—	—	$1,5 \times 10^{-4}$	—	—	—
<i>Merremia</i> spp.	—	—	—	—	—	—	—	$1,3 \times 10^{-3}$	—	—
<i>Zygophyllum stapfii</i>	—	—	—	—	—	—	—	—	—	7×10^{-4}

TABLE 6: The index of utilization of plants displaying defoliation by insects on both the gravel plains (GP) and the river washes (RW) of the Ganas Flats.

	JAN. 1983		MAY 1983		SEPT. 1983		JAN. 1984		MAY 1984	
	GP	RW	GP	RW	GP	RW	GP	RW	GP	RW
<i>Stipagrostis hochstetterana</i>	0,05	0,05	0,3	0,18	0,36	0,08	1,05	—	0,40	0,07
<i>S. uniplumis</i> var. <i>intermedia</i>	0,009	—	0,03	—	—	—	—	—	—	—
<i>S. namaquensis</i>	—	—	—	—	—	—	—	—	—	0,06
<i>Zygophyllum simplex</i>	0,053	—	0,02	—	—	—	—	—	—	—
<i>Lebeckia</i> spp.	—	—	—	0,17	—	—	—	—	—	0,10
<i>Astenatherum</i> spp.	—	—	—	0,03	—	—	—	—	—	—

TABLE 7: Seasonal variations in game numbers on the Ganas Flats between June 1982 and May 1984.

Date	Springbok	Gemsbok	Ostrich	Total
1982				
June	1	8	1	10
August	1	19	5	25
November	49	0	4	53
1983				
January	65	10	0	75
May	7	0	30	37
September	1	3	51	55
1984				
January	1	2	4	7
May	2	7	0	9

intermedia, *S. subacaulis*, *T. triquetra* and *L. platycarpus* appear particularly vulnerable to drought, showing noticeable basal cover decline (Tables 1 & 2). Hardier perennial species such as *S. hochstetterana* were more resilient, displaying more gradual changes to environmental factors. Perennial xerophytic species, such as *Z. stapfii* are the most drought resistant plants in this area, maintaining their basal cover and succulent foliage even throughout the driest periods.

The percentage green material

During this study, the vegetation in the river washes remained consistently greener than that on the surrounding gravel plains (Figure 2). This is attributable to the higher perennial component in the river wash habitat where several species maintained a relatively high index of greenness even during the driest months (Table 4). The overall index of greenness did not im-

prove after the light 1983 rains (Figure 2) although in the river washes *Merremia* spp. and *C. foliosa* showed a slight increase in percentage green material.

Even though no precipitation occurred, both habitats became noticeably greener after September 1983 (Figure 2) when several species displayed an increase in their percentage green material (Tables 3 & 4). This green flush was probably a response by the perennials to the rising summer temperatures.

The 1984 showers, estimated to have been at least 10 mm on the Ganas Flats, brought about a slight recovery of veld conditions (Figure 2). This recovery was most noticeable on the gravel plains where grass species, viz. *S. uniplumis* var. *intermedia* and *S. subacaulis*, showed an increase in percentage green material from zero to 5% and 13% respectively. In addition, several other species became greener (Table 3).

Game numbers, migration and veld utilisation

Viljoen (1980) found that the northern pro-Namib areas were only well utilised by large herbivores during the rainy season, with the majority of game species moving east during the drier months. Similar observations were made in the Namib Park in the central Namib Desert where Nel *et al.* (1985) report that the seasonal migration of game was west to east and back. The westward movement occurred with the onset of rain and the extended eastward migration was made impossible by fences. This situation has resulted in local game overpopulations and overgrazing in areas of the Namib Park (Nel *et al.* 1985).

An inverse trend occurs in the northwestern pro-Namib areas where game numbers on the Ganias Flats are at their lowest directly after the rains, and increase when the area is at its driest (Figure 2). Similarly, there was an increase in the relative herbivore utilisation of the vegetation on both the gravel plains and river washes during the dry summer months preceding the 1984 rains (Figure 4). This occurred even though both crown and basal cover and the index of greenness were at their lowest (Figures 2 & 3). The drop in herbivore numbers observed during May 1983 and January 1984 and the subsequent decrease in herbivore utilisation of vegetation on the Ganias Flats could be as a result of the east-west rainfall gradient typical of the Namib Desert. It appears that most game migrated from west to east immediately after earlier rains which had fallen in the interior promised better pastures inland. This migration took place even though good rains had fallen on the western pro-Namib plains. The return migration from east to west is probably stimulated by desiccation, due to higher temperatures and hot winds, of inland pastures. Thus, it is during the drought periods that the western pro-Namib areas, particularly the river wash habitats, serve as an important food reservoir for large herbivores.

In the pro-Namib a north-south migration, encompassing a movement of game from the plains into the episodic riverine areas, has also been observed. Gemsbok *Oryx gazella* in particular are seen in greater numbers in the Hoanib River during the early summer months where they are believed to feed extensively off *Acacia albida* pods and to seek shelter during the hot, dry season.

During the course of this study the vegetation in the river washes showed consistently higher herbivore utilisation than did the surrounding gravel plains (Figure 4). The results depicted in Tables 3 and 4 show that *S. hochstetterana* and *C. foliosa* were the only two species consistently utilised by herbivores while hardy perennials such as *S. namaquensis*, *A. pechuelli*, *Astenatherum* spp., *O. microcarpum* and *Merremia* spp. provided valuable forage during the drier periods of 1983. *C. foliosa* was the most palatable species encountered and, although relatively scarce on both the gravel plains and in the river, washes, showed consistently high attractance values (Table 5.).

Springbok *Antidorcas marsupialis* were regularly seen in the river washes feeding off *C. foliosa*, *T. oxygona*, *T. dregeana*, *Merremia* spp. and *Z. stapfii*. Gemsbok were not seen feeding, but their preference for the gravel plains as opposed to the river washes suggests a diet comprising mostly of grass. In particular, *S. hochstetterana* regularly showed characteristic signs of gemsbok utilisation as described by Van Zyl (1965). Although utilisation of vegetation by ostrich *Struthio camelus* was difficult to detect and quantify, these birds were often seen feeding on *Z. simplex* and the flowers of *O. microcarpum* in the river washes. Utilisation of vegetation by rodents, which is believed to be

substantial in other areas (Curtis & Perrin 1979), was not quantified during this study although Cape hares *Lepus capensis* were often encountered in the river washes. Signs of vegetation utilisation by this species as described by Smithers (1983), were noted amongst the larger perennial grasses such as *Astenatherum* spp. and *S. namaquensis*, particularly where roots or new growth had been exposed. Smaller rodents were infrequently observed but signs of their presence were evident in the river washes where plants such as *Geigeria spinosa* appeared to have been utilised.

Game numbers in Kaokoland and the Skeleton Coast Park have decreased dramatically since the early 1970's due to competition with domestic stock, severe droughts and poaching (Viljoen 1980; 1982 a; 1982 b). Table 7 shows the low density of game counted in the study area between 1982 and 1984 and Tables 3 and 4 show that minimal utilisation of the veld occurred during the period. Thus, it appears that preferred forage species were selected by herbivores while the more abundant species were largely ignored. Of some of the key pasture species viz. *S. uniplumis* var. *intermedia*, *S. subacaulis* and *G. spinosa*, only *S. uniplumis* var. *intermedia* displayed signs of game utilisation (Table 3). During the dry months although still abundant, the nutritional value of this species declined considerably and showed no signs of further utilisation.

Termites and wind play an important role in vegetation defoliation (Nel *et al.* 1985). All but obvious insect utilisation was difficult to detect and quantify. *S. hochstetterana* was the only species that showed noticeable signs of insect defoliation on a regular basis (Table 6). The grasses on the gravel plains showed a higher degree of insect utilisation than did the river wash plant species and overall utilisation appears to have been at its highest during the hot, dry season ending in January 1984.

CONCLUSION

Between 1982 and 1984 rainfall occurred sporadically over the northern pro-Namib and the vegetation cover on the Ganias Flats declined significantly in the absence of annual showers. In particular the gravel plains, with their high proportion of annual grasses became largely devoid of vegetation during the dry months.

An increase in game numbers and subsequent veld utilisation occurred on the Ganias Flats during periods of drought when the river washes, which were characteristically greener and more substantially vegetated than the surrounding gravel plains, supplied herbivores with valuable forage. In view of the low game numbers encountered and accounts of substantial game herds occurring in the past, it appears that the northwestern pro-Namib plains are understocked at present and only a small fraction of the suitable forage is utilised.

Provided seasonal game movements between the

Skeleton Coast Park and the interior remain unrestricted, the northwestern pro-Namib areas should continue to act as an important food reservoir for the game of this region, particularly during times of drought. Thus, any attempts to erect a game-proof fence along the eastern boundary of the Skeleton Coast Park should be avoided in the interests of the long term ecological future of this region.

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Branching patterns in *Aloe dichotoma* – is *A. ramosissima* a separate species?

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ABSTRACT

The proposal that *Aloe ramosissima* be reduced to varietal rank under *A. dichotoma*, based on a low incidence of *ramosissima*-type branching pattern (less than 100 mm above ground level) in most *A. dichotoma* populations, is invalid, as the *ramosissima*-type branching pattern has a different cause in the two taxa. Branching patterns in *A. dichotoma* populations show a majority of first branchings at between 1.5 m and 2.5 m above ground. Branching below 1 m in *A. dichotoma* populations is caused by ungulate destruction of the apical meristem, whereas in *A. ramosissima* branching below 1 m is initiated by spontaneous meristematic division.

INTRODUCTION

Aloe dichotoma Masson is one of three species in the section *Dracoaloe* Berger of the genus *Aloe*. The *Dracoaloe* are characterized by dichotomous branching and cylindric-ventricose, fleshy, yellow flowers about 33 mm long (Reynolds 1982). The three species (*A. dichotoma*, *A. ramosissima* Pillans and *A. pillansii* L. Guthrie) are differentiated by their height and degree of branching, leaf size, and orientation of inflorescences. All three species are confined to dry, rocky areas: *Aloe dichotoma* is the most widespread, occurring in the northwestern Cape Province, South Africa, and southern South West Africa/Namibia (its southern distributional range), and isolated populations at Brandberg (Jankowitz 1977; Reynolds 1982). Both *A. ramosissima* and *A. pillansii* are confined to a few populations in the northern Richtersveld and near Rosh Pinah in the Luderitz magisterial district of South West Africa/Namibia.

Aloe dichotoma grows to 9 m tall, with a trunk of about 1 m diameter, and has pronounced dichotomous branching above this height. The leaves are 250–350 mm long and 50 mm broad at the base. The inflorescence is a branched panicle, up to 300 mm long, and usually branched into three (occ. 4 or 5) racemes. *Aloe ramosissima* differs in being shorter, up to 3 m tall, and in branching at a height of less than 600 mm. It also has smaller leaves, 150–200 mm long and about 22 mm broad at base, thinner branches and smaller rosettes of leaves at the branch tips. However, it is indistinguishable from *A. dichotoma* on inflorescence and floral characters (Reynolds 1982), and on microscopic leaf characters (Glen & Hardy 1987).

Recently, Glen & Hardy (1987) proposed that *Aloe ramosissima* be reduced to varietal rank under *A. dichotoma* Mason as *A. dichotoma* Mill. Although based on microscopic and macroscopic data, their

major argument is that the branching from near ground level, the major diagnostic feature of *A. ramosissima*, occurs at low levels in all populations of *A. dichotoma* (H.F. Glen pers. comm.).

The aims of this study were to investigate the levels of branching in *A. dichotoma* in its southern distributional range and to determine whether the pattern of branching differed among populations and between *A. dichotoma* and *A. ramosissima*.

METHODS

Eleven populations of *A. dichotoma* Masson were sampled in southern South West Africa/Namibia and the northwestern Cape (Figure 1) during July 1987. Sampling was undertaken on a minimum of 100 live

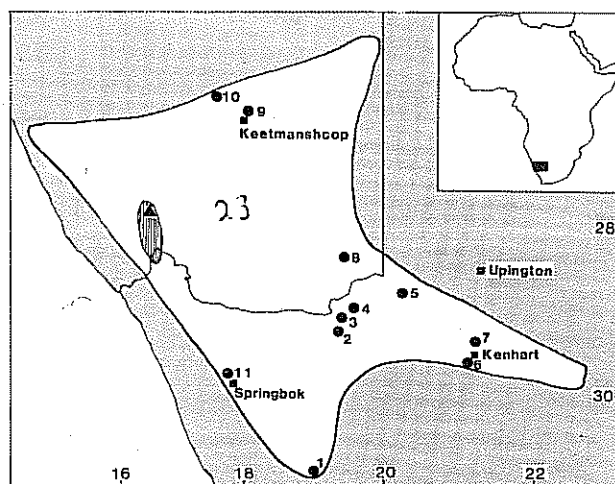


FIGURE 1: Location of populations of *Aloe dichotoma* (●) and *A. ramosissima* (▲) investigated in this study. Locality names are given in Table 1. The unshaded area denotes the southern distributional range of *A. dichotoma* based on herbarium records and Jankowitz (1977). Similarly, the hatched area denotes the distributional range of *A. ramosissima*.

plants in an area not less than 500 m by 500 m, or, where assemblages consisted of fewer than 100 plants, the entire population. In each population, plants' absolute height, height to first branching, and the number of branching occurrences were determined. Only a single population of *A. ramosissima* was visited. Due to lack of field time, height to first branching in this species was estimated from photographic records.

RESULTS

The proportion of *A. dichotoma* plants branching below 1 m varied among populations from 0 to 45% (Figure 2). This proportion was significantly and positively correlated with the proportion of the population less than 1 m tall ($r = 0.60$, $p < 0.05$). The distribution of height to first branching showed distinct primary peaks at between 1.5 and 2.25 m, with smaller secondary peaks at 0.25–0.75 m in all populations with appreciable numbers of plants shorter than 1 m. However, among populations there was no correlation between the average height of plants taller than 1 m and their average height to first branching ($r = 0.17$, $p > 0.5$).

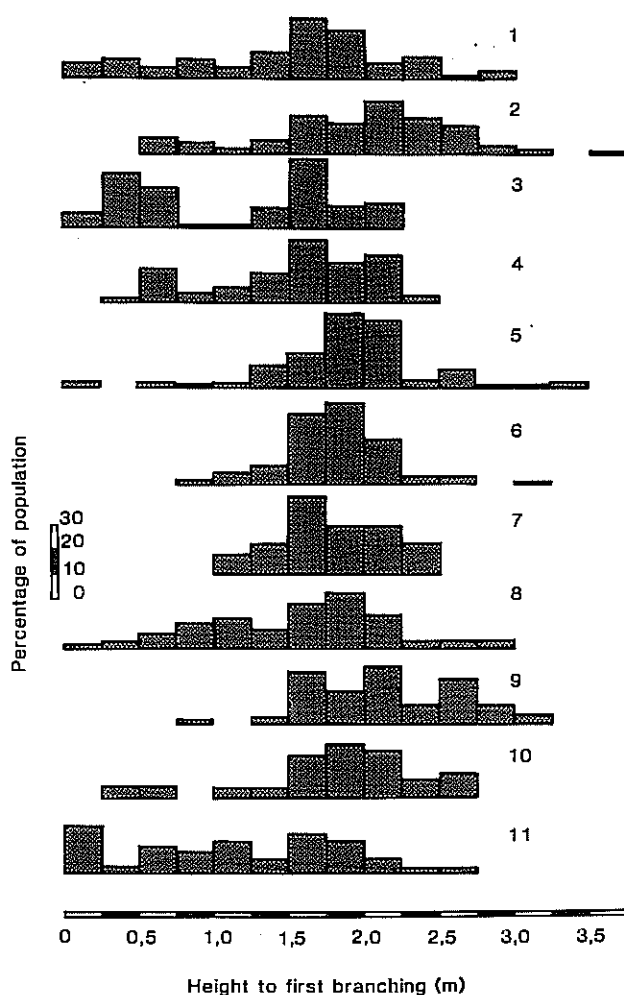


FIGURE 2: Proportion of first branching of *Aloe dichotoma* in different height classes for populations at the southern portion of its distributional range.

The geographical distribution of branching patterns is shown in Figure 3. Eastern populations had fewer plants branching below 1 m than those in the west and south.

The proportion of plants less than 1 m tall that were damaged in the different populations varied between 0 and 51% (Table 1). Damage was largely due to ungulates breaking off tops of plants, presumably when browsing the apical meristems. However, such browsing, by goats, was only positively identified at Onseepkans ($28^{\circ}57'S$, $19^{\circ}24'E$). At Snyfontein ($26^{\circ}30'S$, $17^{\circ}51'E$) 26% of the plants had stems gnawed by donkeys and horses, apparently as a source of water (D. Clark pers. comm.), and 3% of aloes greater than 1 m tall (average 1.25 m) had been knocked over within the

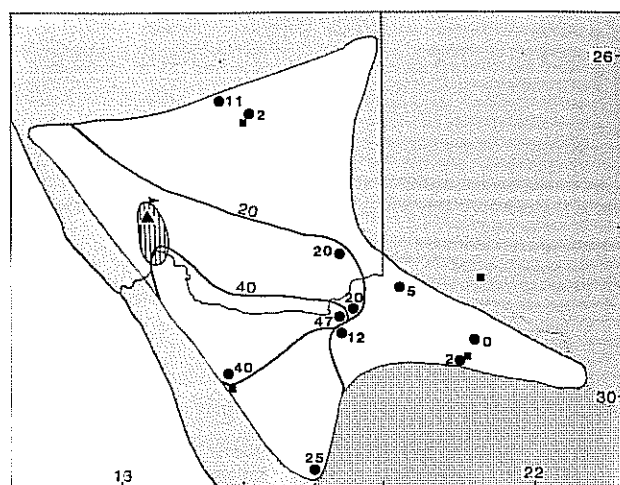


FIGURE 3: Geographical variation in the proportion of *Aloe dichotoma* plants per population branching below 1 m height (given for each site). Extrapolation of isodendrons into the Richtersveld is based on Reynolds (1982).

past year. There were no significant differences between height to first branching in damaged plants less than 1 m tall and the height to damage in those which either died as a consequence thereof or were damaged too recently to have branched (t -test, $P > 0.05$, Onseepkans) (Table 1). The height at which plants less than 1 m branched was significantly higher in areas containing goats than those containing sheep (t -test, $P < 0.05$). There were no undamaged plants which branched below 1 m.

All plants in the single population of *A. ramosissima* visited branched below 0.3 m. All plants less than 1 m tall branched below 0.1 m. No damage by herbivores was evident.

DISCUSSION

True dichotomous branching (by apical meristem division) is rare in the Monocotyledonae (Tomlinson *et al.* 1970). Schoute (1918) investigated branching patterns in *Aloe succotrina* Lam and concluded that branching in *Aloe* is always triggered by the formation of a terminal inflorescence, i.e. the branching is pseudodichoto-

TABLE 1: Number of plants less than 1 m tall showing signs of damage or branching and the mean height of damaged plants in 11 populations of *Aloe dichotoma*. All the plants which had branched below 1 m tall were damaged. Plants above 1 m tall were not included as it is not usually possible to determine the cause of first branching.

Population	Total plants < 1 m tall (A)	Damaged plants		Mean (\pm SD) height (mm)		Agents
		branched (% of A)	unbranched (% of A)	to branching	to damage ¹	
1 Klipdrift	86	8	0	234 \pm 96	—	Sheep
2 Poffadder	15	0	7	—	0	Goats
3 Onseepkans	65	26	25	402 \pm 146	418 \pm 268	Goats
4 Skietskipkop	45	9	0	495 \pm 134	—	Goats
5 Augrabies	14	7	0	190	—	Goats
6 Kenhardt	1	0	0	—	—	Goats
7 Strausheim	8	0	0	—	—	Sheep
8 Kokerboom	0	—	—	—	—	Sheep
9 Keetmanshoop	3	0	0	—	—	Goats
10 Snyfontein	39	15	0	408 \pm 217	—	Donkeys, horses & Goats
11 Springbok	71	4	1	219 \pm 168	400	Sheep

¹ Including both dead and recently damaged plants.

mous. In the case of branching in *A. dichotoma* (and presumably the section *Dracoaloe*), two side-branches emerge below the terminal inflorescence which usually dies while only a few mm long in the first few branchings (Schoute 1918; pers. obs.). In *A. dichotoma* apparently dichotomous branching from the two topmost lateral buds may also occur following damage to the apical meristem (pers. obs.).

Branching patterns in *A. dichotoma* show a bimodal distribution with the majority of first branchings occurring between 1.5 and 2.5 m. This natural branching is quite distinct from the branching which occurs between 0.1 and 0.9 m, which is largely caused by destruction of the apical meristem by ungulates. Goats appear to eat apical meristems, whereas some damage may be caused by trampling activities of goats and other ungulates. Plants over 1 m tall were apparently safe from destruction by sheep and goats, although horses and donkeys occasionally damaged plants up to 1.5 m tall, usually by knocking them over. The height of damage and its variation between areas containing sheep and goats may reflect either browsing height preferences or damage done by animals trampling over plants and breaking off their tops. The production of axillary buds in the remaining leaves generally follows, giving rise to 2–3 (occ. up to 7) branches. Although not always a dichotomous branching pattern, it is difficult to distinguish such branching from dichotomous branching when specimens have matured.

The pattern of branching between the *A. ramosissima* and *A. dichotoma* populations investigated differs considerably. In the former all plants below 1 m tall appear to branch spontaneously, whereas any branching at comparable heights in the latter appears to be largely due to damage by ungulates. The inclusion of *A. ramosissima* into *A. dichotoma*, based on a small proportion of plants with *A. ramosissima* branching patterns in all *dichotoma* populations, is therefore questioned, as the branching has different causes.

A further complication results from the spatial distribution of young *A. dichotoma* plants: seedlings may occur in clumps of up to six plants in favourable microhabitats (pers. obs.). Although young plants in such clumps are distinct, the stems may fuse with age and thus appear to branch from the base of 'single' mature specimens. As plants age this apparent height of branching increases as fusion progresses. This 'pseudobranching' was proposed by Reynolds (1982) to account for the proportion of *ramosissima* types in *A. dichotoma* populations.

Furthermore, the proposed rank of *variety* cannot be upheld. Since the distribution of the spontaneously low-branching *ramosissima* taxon is geographically distinct (Reynolds 1982) and does not occur in all *A. dichotoma* populations, as suggested by Glen and Hardy (1987), *ramosissima* must be ranked as either a species or subspecies. Reynolds (*loc. cit.*) states that there appear to be hybrid populations south of Ku-boos. Unfortunately we were unable to visit the Richtersveld, and thus could not determine whether the branching patterns in these populations may be due to hybridization or ungulate damage. The high grazing levels in the Richtersveld (A. Le Roux pers. comm.) warrant a closer investigation of the latter possibility. The two taxa are quite distinct in the northern Richtersveld (Reynolds 1982) and north of Rosh Pinah (pers. obs.) where they coexist without any apparent hybridization (Jankowitz 1972, 1977). Whether *A. ramosissima* has sufficient distinguishing characters to warrant the status of a separate species, is beyond the scope of this paper.

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The identification of hybrids of *Barbus aeneus* X *B. kimberleyensis* and *Labeo capensis* X *L. umbratus* in Hardap Dam, SWA/Namibia

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ABSTRACT

A morphometric and biochemical genetic comparison of *Barbus aeneus* and *B. kimberleyensis* with *B. cf. kimberleyensis* from Hardap Dam, SWA/Namibia, revealed that the latter population showed distinct evidence of hybridization between *B. aeneus* and *B. kimberleyensis*. A similar comparison of the three *Labeo*-populations from Hardap Dam also indicated hybridization between *L. capensis* and *L. umbratus*. It was also possible to identify *L. capensis* x *L. umbratus* individuals, according to electrophoresis, that have been identified as "pure" specimens with the aid of morphometric and meristic characteristics.

INTRODUCTION

Large cyprinids of the genera *Barbus* and *Labeo* are among the most valuable freshwater fishes all over Africa (Jackson & Coetzee 1982). According to these authors, labeos are greatly esteemed as food in most parts of tropical Africa, while in South Africa the yellowfishes *Barbus aeneus* and *B. kimberleyensis* are among of the most highly regarded of our indigenous freshwater angling species. Despite the economic importance of these species, their continued existence as pure species are being threatened by hybridization.

In Hardap Dam, SWA/Namibia, the genus *Labeo* is represented by *L. capensis* and *L. umbratus* as well as a range of intermediate forms due to certain morphological characteristics. The genus *Barbus* however is represented by a single population described by Gaigher (1976) as *B. cf. kimberleyensis*, but recently it has been referred to as *B. aeneus* (Schrader 1986). To prevent confusion, this population will be referred to as *B. cf. kimberleyensis* in this paper. In an attempt to determine the taxonomic status of the Hardap Dam populations (*Labeo* and *Barbus*), morphometric, meristic and electrophoretic comparisons were performed between the intermediate forms and the pure populations of each species. Due to the fact that only one *Barbus* population exists in the Hardap Dam, pure populations of *B. aeneus* and *B. kimberleyensis* were collected from the Vaal River for comparison. It was also possible to determine the genetic distance between the two intermediate forms and the pure species, using electrophoresis as it has proven itself a useful complement to traditional systematic methods (Grant & Leslie 1983; Stratil *et al.* 1983).

MATERIALS AND METHODS

Specimens were collected at three locations in southern Africa. Both intermediate forms as well as the *Labeo* species were collected in the Hardap Dam (17°57'E, 24°37'S) using gill and seine nets. *B. aeneus* was collected in the Vaal River near the Barrage, while *B. kimberleyensis* was collected in the Vaal Dam. Samples of skeletal muscle and blood serum were collected as described by Mulder (1986) and Van Vuuren (1986)

and stored at -20°C for later electrophoretic analysis.

Morphometric and meristic characteristics which were determined are the following:

- Scale counts on the lateral line and around the caudal peduncle.
- Number of spines and rays in the dorsal and anal fins.
- Gillraker counts
- Vertebrae counts
- Standard length/Body depth (SL/BD)
- Head length/Eye diameter (HL/ED)
- Head length/Head width (HL/HW)
- Standard length/Head length (SL/HL)
- * Snout length/Opercular groove (SN/OG)
- * = Performed on *Barbus* only.

Electrophoretic analysis:

Polyacrylamide gel electrophoresis:

Serum transferrin and serum esterase phenotypes were determined by using a 6% vertical, tris-citrate buffer system (Table 1) as described by Avtalion and Wojdani (1971) and Van der Bank (1984).

Starch gel electrophoresis:

Horizontal starch gel electrophoresis were used to detect the banding patterns of nine muscle proteins (Table 1). The gels consisted of a 13% hydrolyzed potato starch (Sigma, S-4501). The gel constitution was applied as described by Smith (1976) and tissue preparation by May *et al.* (1979).

Three buffer systems were used to achieve maximum resolution of the protein bands on the gels:

- RW:** gel: TRIS 0,03M, citric acid 0,005M (pH 8,5).
tray: Lithium hydroxide 0,06M, boric acid 0,3M (pH 8,1). (Rideway *et al.* 1970).
- TC:** gel: 1:15 dilution of tray solution.
tray: Citric acid 0,05M, Tris 0,15 (pH 6,9). (Whitt 1970).
- MF:** gel: 1:4 dilution of tray solution.
tray: TRIS 0,18M, boric acid 0,1M, EDTA 0,004M (pH 8,7). (Markert & Faulhaber 1965).

TABLE 1: Summary table of proteins screened in *Labeo umbratus*, *L. capensis* and their intermediate form as well as *Barbus aeneus*, *B. kimberleyensis* and their intermediate form. In each case the buffer system which gave best resolution, the number of loci coding for each protein and the genus which were examined using the specific protein, are given.

Protein	Abbr.	E.C. No.	Buffer	Loci scored	Genus
Adenylate kinase	AK	2.7.4.3	TC	1	B
Esterase (serum)	EST	3.1.1.1	Tris/citrate	1	L,B
Glyceraldehydephosphate dehydrogenase	GAP	1.2.1.12	RW	2	L
Glycerol-3-phosphate dehydrogenase	GPD	1.1.1.8	RW	2	L
Isocitrate dehydrogenase	IDH	1.1.1.42	MF	2	L
Lactate dehydrogenase	LDH	1.1.1.27	RW/TC	2	L,B
Malic enzyme	ME	1.1.1.40	MF	2	B
Purine nucleoside phosphorylase	NP	2.4.2.1	RW	1	B
Superoxide dismutase	SOD	1.15.1.1	MF	1	B
Transferrin (serum)	TF	—	Tris/citrate	1	L,B

L: *Labeo* — B: *Barbus*

Allelic nomenclature was applied as described by Ailendorf and Utter (1979).

Statistical procedures

Morphometry and meristics

The mean and standard deviation were determined for all characteristics. These data were also tested for normal distribution (95% probability) by using the *Chi-square* test.

Electrophoresis

Numbers of observed phenotypes at each locus were tested for deviations from Castle-Hardy-Weinberg proportions using the log-likelihood-statistic *G*, for goodness of fit (Sokal and Rohlf 1969). The genetic distance, *D*, (Nei 1972) and its standard deviation (Nei & Roychoudhury 1974), were determined for each population using all loci. Finally the average population heterozygosity was determined as described by Grant (1985).

RESULTS AND DISCUSSION

Morphometric and meristic analysis

The results obtained for the *Barbus* population are presented in Table 2 and 4 and those for the *Labeo* populations in Table 3 and 5 and Figure 1.

Comparing the lateral line and peduncle scale counts of the *Barbus* populations with that found in the literature (Barnard 1943; Groenewald 1958), shows the same degree of variation within species from different localities.

As it is known that these differences can be induced by environmental conditions (Wallace 1973), it was not possible to determine the taxonomic status of the Hardap Dam *Barbus* population using the characteristics.

The same applies to the dorsal and anal rays and spines (Table 2). Of *B. kimberleyensis* 88% had nine rays in the dorsal fin, while 94% and 90% of individuals of respectively *B. aeneus* and *B. cf. kimberleyensis* had eight rays in the dorsal fin. Although it seems that there is a greater similarity between the last two populations, much variation within a species at

different locations were recorded. Barnard (1943) found that two out of every three individuals of *B. aeneus*, which were collected from the Fish River near Gibeon, had nine rays in the dorsal fin. From a total of 103 individuals of the same species collected from the Oranje River near Goodhouse, only six had eight rays, while the rest had nine rays in the dorsal fin.

Variation of morphological characteristics among localities were again emphasized by the gill raker count. The Hardap Dam population, which might be a pure population of either *B. aeneus* or *B. kimberleyensis* or an intermediate form, had a mode lower than the first mentioned two populations.

Vertebral counts included the Weber-apparatus as one element. Although it seems that *B. cf. kimberleyensis* has greater similarity with *B. aeneus* concerning this characteristic, it cannot be taken for granted, as Var der Bank (1984) found that a higher water temperature produced individuals with less vertebrae.

Considering that all three *Barbus* populations differ in locality, the possibility of environmentally induced morphological differences between the three populations cannot be excluded. No meaningful conclusion can thus be made before more populations of each species has been studied at different locations. The fact that *B. aeneus* and *B. kimberleyensis* are quite closely related makes useful conclusions all the more difficult.

The standard length/head length, determined for *B. cf. kimberleyensis* (Table 4), had a range overlapping with the ranges of both *B. aeneus* and *B. kimberleyensis*. This indicates intermediate characteristics which is an indication of hybridization.

The standard length/body depth, head length/eye diameter, as well as the head length/head width of a three populations stretches over a very narrow range (Table 4), with *B. cf. kimberleyensis* having either the highest or lowest mean. This again illustrates the influence of the environment on external characteristics but it is also an indication of the high degree of similarity between *B. aeneus* and *B. kimberleyensis*.

TABLE 2: Meristic data of the three *Barbus* populations with sample size, range and mode.

	<i>B. aeneus</i>			<i>B. cf. kimberleyensis</i>			<i>B. kimberleyensis</i>		
	N	Range	Mode	N	Range	Mode	N	Range	Mode
Lateral line count	51	38-46	42	61	39-47	42	33	38-45	42
Caudal peduncle count	51	15-17	16	61	15-17	16	33	15-18	16
Gill raker count	51	14-18	16	61	10-7	13,5	33	11-18	14
Dorsal spines, rays	51	iv7-9	8	61	iv8-9	8	33	iv8-9	9
Anal spines, rays	51	iii5	5	51	iii5	5	33	iii4-5	5
Vertebral count	10	39-41	50	10	38-41	40	19	38-40	39

TABLE 3: Meristic data of the three *Labeo* populations with sample size, range and mode.

	<i>L. capensis</i>			<i>L. capensis x L. umbratus</i>			<i>L. umbratus</i>		
	N	Range	Mode	N	Range	Mode	N	Range	Mode
Lateral line count	33	33-48	45	51	44-54	47	30	49-60	55
Caudal peduncle count	33	20-25	22	51	21-32	26	30	28-36	32
Gill raker count	33	42-53	48	51	43-57	49	30	43-53	47
Dorsal spines, rays	33	iii10-11	10	51	iii9-10	9	30	iv9-10	9
Anal spines, rays	33	iii5	5	51	iii5	5	30	iii5	5
Vertebral count	33	39-41	40	51	39-41	40	30	39-40	39

TABLE 4: Morphometric data of the three *Barbus* populations with sample size, mean and standard deviation.

	N	<i>B. aeneus</i>	N	<i>B. cf. kimberleyensis</i>	N	<i>B. kimberleyensis</i>
SL/BD	51	4,233 + 0,205	61	4,362 + 0,616	33	4,209 + 0,207
HL/ED	51	6,641 + 0,677	61	5,774 + 0,863	33	8,259 + 1,375
HL/HW	51	1,515 + 0,099	61	1,950 + 0,280	33	1,757 + 0,099
SL/HL	51	4,641 + 0,239	61	4,419 + 0,633	33	3,930 + 0,197
SL/GL	51	3,28 + 0,767	61	2,35 + 0,671	33	1,63 + 0,332
SN/OG	51	1,422 + 0,135	61	1,294 + 0,127	33	0,916 + 0,103

TABLE 5: Morphometric data of the three *Labeo* populations with sample size, mean and standard deviation.

	N	<i>L. capensis</i>	N	<i>L. capensis x L. umbratus</i>	N	<i>L. umbratus</i>
SL/BD	33	4,159 + 0,323	51	4,040 + 0,260	30	3,955 + 0,196
HL/ED	33	7,397 + 1,428	51	9,633 + 0,916	30	10,325 + 1,101
HL/HW	33	1,579 + 0,145	51	1,600 + 0,077	30	1,508 + 0,103
SL/HL	33	4,507 + 0,352	51	4,349 + 0,237	30	4,022 + 0,208

B. aeneus and *B. kimberleyensis* can be distinguished from each other by using the ratio of snout length/distance from the eye to the opercular groove. The same applies to the ratio of gut length/standard length. The results obtained for these ratios again indicate possible hybridization in Hardap Dam, because *B. cf. kimberleyensis* had intermediate ranges.

Figure 1a shows the external morphology of *L. umbratus*, the typical intermediate forms and *L. capensis*. The external morphology of the intermediate forms varies, but the head generally resembles that of *L. umbratus* whilst the body is more *L. capensis*-like. The mouth varies from terminal to sub-inferior when

opened, but never inferior as in *L. capensis* (Figure 1b). The same tendency was observed by Gaigher and Bloemhof (1975) for the hybrids that they have described from Hardap Dam.

The results presented in Table 3 show that there is no significant difference between the three populations in terms of the number of gill-rakers on the anterior gill-arch, the number of vertebrae as well as the number of spines and rays in the anal fin. But when comparing the scale counts on the lateral line and around the caudal peduncle, it is possible to distinguish between a population with a lower scale count (*L. capensis*) and one with a higher scale count (*L. umbratus*) as well as

a third population which overlaps with the scale counts of both the other two populations. When a further comparison is made of these scale counts, it is clear that the mode of the number of scales on the lateral line of the intermediate population, is closer to that of *L. capensis*, while the mode of the caudal peduncle is intermediate to that of *L. capensis* and *L. umbratus*.

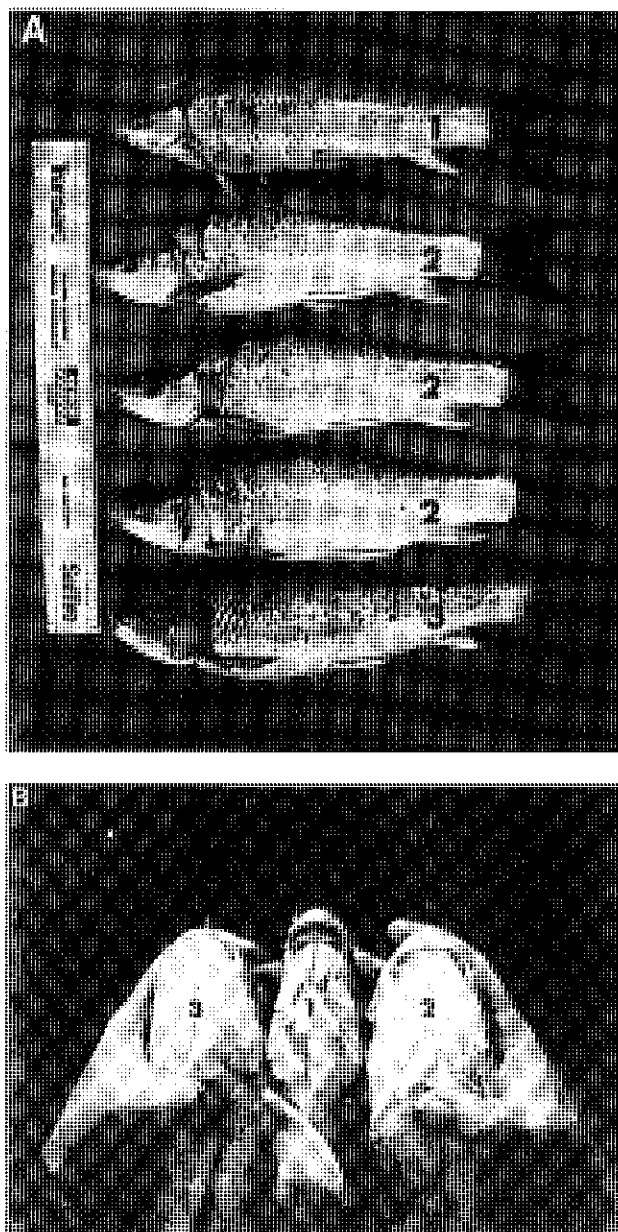


FIGURE 1: A. *Labio capensis* (1), *L. umbratus* (3) and the intermediate forms (2) collected from the Hardap Dam.

B. The mouth position of *L. capensis* (1), *L. umbratus* (3) and the intermediate form (2).

The same tendency as above, is observed when the meristic data in Table 5 are compared. It is therefore of interest to note that the intermediate forms are closer to *L. umbratus* in some features (eye diameter, head width, head form), intermediate in other features (position of the mouth, number of scales around the

caudal peduncle, head length) and closer to *L. capensis* in still other features (number of scales on lateral line and spines in the dorsal fin). Thus, according to this morphometric and meristic comparison, it seems that these intermediate forms could indeed be hybrids between *L. capensis* and *L. umbratus*. But it is also clear that none of these characteristics could be used alone to identify a single hybrid unambiguously. For this reason these populations have been analysed electrophoretically, as this technique has proved itself to be useful in distinguishing between hybrids and closely related species (Valenta 1978; Allendorf & Utter 1979).

Electrophoretic analysis

The products of the different protein coding loci were examined for Mendelian variation. In the *Barbus* populations eight of the loci were monomorphic (LHD-1; LHD-2; ME-1; ME-2; AK-1; NP-1; NP-2 SOD), while the other two were polymorphic (TF EST) (Table 6). In the *Labeo* populations four of these loci were monomorphic (LDH-1; LDH-2; GAP-1 and GPD-1), while the other six were controlled by one or more polymorphic loci (TF; EST; IDH-1; IDH-2 GAP-2 and GPD-2).

Banding patterns in the *Barbus* population:

Serum transferrins (TF)

Banding patterns of *B. kimberleyensis* and *B. cf. kimberleyensis* are quite simple in contrast to that of *B. aeneus*. The fact that both former populations possess only the 90 and 100 allele, suggest a marked similarity between these two populations concerning the transferrin locus. *B. cf. kimberleyensis* had a small excess of heterozygotes. This strongly suggest hybridization in Hardap Dam as it is known that hybridization leads to an increase in heterozygotes in a population (Stratil *et al.* 1983). The excess heterozygotes is especially significant when taking into account that this is an isolate population with a relatively small gene pool which may have led to inbreeding with a resulting decrease in heterozygotes.

Serum esterase (EST)

The three *Barbus* populations all had a single polymorphic locus with double banded heterozygotes and single banded homozygotes. This suggests a monomeric enzyme structure. A total of four bands were visible on the gel, but the 96 band were absent from the *B. aeneus* and the 95 band from the *B. kimberleyensis* populations.

The *B. cf. kimberleyensis* population had the full complement of bands. This again is an indication of hybridization as bands unique for *B. aeneus* and *B. kimberleyensis* were found in the *B. cf. kimberleyensis* population.

Lactate dehydrogenase (LDH)

The three *Barbus* populations all had five bands reflecting the gene products of two loci where the three

TABLE 6: Allelic frequencies of electrophoretic variants of *B. aeneus*, *B. cf. kimberleyensis* and *B. kimberleyensis*. Alleles are designated by their mobilities relative to the common allele.

Locus	Allele	<i>B. aeneus</i>	<i>B. cf. kimberleyensis</i>	<i>B. kimberleyensis</i>
TF	90	—	0,365	0,365
	100	0,394	0,635	0,635
	105	0,154	—	—
	113	0,144	—	—
	120	0,154	—	—
	128	0,154	—	—
	N	52	60	33
EST	88	0,212	0,217	0,442
	95	0,442	0,017	—
	96	—	0,442	0,212
	100	0,346	0,325	0,346
	N	52	60	33
LDH-1	100	1,0	1,0	1,0
	N	52	60	33
LDH-2	100	1,0	1,0	1,0
	N	52	60	33
ME-1	100	0,5	0,5	0,5
	189	0,5	0,5	0,5
	N	52	60	33
ME-2	100	0,5	0,5	0,5
	139	0,5	0,5	0,5
	N	52	60	33
AK	100	1,0	1,0	1,0
	N	52	60	33
NP-1	100	1,0	1,0	1,0
	N	52	60	33
NP-2	100	1,0	1,0	1,0
	N	52	60	33
SOD	92	—	—	1,0
	100	1,0	1,0	—
	N	52	60	33

central bands represented the heterotetrameric product between the two loci. These zones of activity were identical in migration speed as well as banding patterns for all three populations.

Malic enzyme (ME)

Two zones of activity were observed for all three *Barbus* populations. ME-1 consisted of only five-banded phenotypes. The second zone of lesser activity had three bands. The low intensity of the bands might indicate that this locus is of mitochondrial origin.

Again the three populations were identical in migration rates as well as banding patterns.

Adenylate kinase (AK)

A monomorphic locus with single-banded homozygotes was expressed in the three populations investigated. Although five bands were observed for all samples, four were identified as satellite bands on the basis of band intensities.

Purine nucleoside phosphorylase (NP)

Two monomorphic loci with two heterotrimeric bands were observed for all *Barbus* populations investigated.

Superoxide dismutase (SOD)

A single zone of banding, with only homozygotes appeared in the gel. The enzymes of *B. aeneus* and *B. cf. kimberleyensis*, however, had a higher migration speed than that of *B. kimberleyensis*. This implies a definite similarity between the former two populations.

Banding patterns in the *Labeo* populations

Serum transferrins (TF)

A single zone of activity was observed for all three populations. In this zone several different single- and double banded phenotypes reflected the products of four alleles (Table 7). No significant departures from the Castle-Hardy-Weinberg proportions were detected for the two "pure" populations, but the intermediate population shared an excess of heterozygotes. Such an

excess of heterozygotes was also observed for hybrids of *Barbus barbuis* and *Barbus meridionalis petenyi* by Stratil *et al.* (1983).

Serum esterases (EST)

A single zone of activity, having single banded homozygotes and double banded heterozygotes, was observed. "Ghost bands" were observed for all the variants and care must therefore be taken not to attribute any genetic value to these bands, as it will give an erroneous impression of the genetic structure of a specific population (Kirpichnikov 1981).

The fastest band (A) showed the highest frequency in the *L. capensis* population, while the slowest band (D) showed the highest frequency in the *L. umbratus* population. It is of interest to note, however, that these two bands showed almost the same frequency in the intermediate population. This phenomenon is surely evidence for hybridization between these two populations. This hybridization is further emphasized by the

low frequency of D-bands that were observed in the *L. capensis* population and A-bands in the *L. umbratus* population, probably because of individuals that were wrongly identified as pure, while being hybrids. This is supported by the fact that no D-bands and A-bands were observed respectively in pure populations of *L. capensis* and *L. umbratus* (Van Vuuren *et al.* in press). Hybridization between these two populations is still further emphasized by the excess of heterozygotes that were observed in the intermediate population.

Lactate dehydrogenase (LDH)

Two zones of activity that appeared to reflect the products of two loci, were observed for all three populations. Both loci showed only the one homozygote but heterotetrameric bands were visible between these two loci. No variance in the mobility of the homozygotes, of the different populations, was visible.

Isocitrate dehydrogenase (IDH)

The products of two loci appeared in all three popula-

TABLE 7: Allelic frequencies of electrophoretic variants of the three *Labeo* populations in Hardap Dam. Alleles are designated by their mobility relative to the common allele.

Locus	Allele	<i>L. capensis</i> x <i>L. umbratus</i>	<i>L. capensis</i>	<i>L. umbratus</i>
TF	84	—	—	—
	93	—	—	—
	100	0,636	0,500	0,983
	109	0,061	0,333	—
	113	0,030	—	—
	116	0,273	0,167	0,017
	122	—	—	—
	N	33	51	30
EST	100	0,076	0,529	0,967
	103	0,045	—	—
	108	0,879	0,471	0,033
	113	—	—	—
	N	33	51	30
LDH-1	100	1,0	1,0	1,0
	N	33	51	30
LDH-2	100	1,0	1,0	1,0
	N	33	51	30
IDH-1	77	0,121	0,520	0,917
	100	0,879	0,480	0,083
	N	33	51	30
IDH-2	84	—	0,5	0,933
	100	1,0	0,5	0,067
	N	33	51	30
GAP-1	100	1,0	1,0	1,0
	N	33	51	30
GAP-2	100	0,045	0,049	0,050
	115	0,955	0,951	0,950
	N	33	51	30
GPD-1	100	1,0	1,0	1,0
	N	33	51	30
GPD-2	100	0,091	0,108	0,900
	120	0,909	0,892	0,100
	N	33	51	30

tions (Table 7), where heterodimeric bands did not form between the loci. IDH-1 stained more intense than IDH-2 in the skeletal muscle, but according to Grant and Leslie (1983), IDH-2 will stain more intense in liver. A two banded heterozygous phenotype was consistent, which is unexpected for dimeric enzyme. But these two banded heterozygotes for IDH were also observed by Grant and Leslie (1983) for *Lophius u-*
sicephalus.

It is not surprising that the intermediate population shows again an excess of heterozygotes. It is however conspicuous that the fast migrating allele (A) shows the highest frequency in the *L. capensis* population, while the frequency for these two alleles are about the same intermediate population (Table 7). IDH confirms thus the possibility of hybridization between *L. capensis* and *L. umbratus* in Hardap Dam.

Glyceraldehyde-phosphate dehydrogenase (GAP)

Two zones of activity were observed, where heterotetrameric bands did form between the loci. GAP-1 was monomorphic for all three populations as only one homozygote was observed for all the individuals. GAP-2 was polymorphic for three alleles that produced one single and one triple-banded phenotype. GAP-2 did not show the same intensity as GAP-1 in skeletal muscle, but will probably show a higher activity in liver (Philip *et al.* 1983; Grant 1985)

Glycerol-3-phosphate dehydrogenase (GPD)

Two zones of banding were observed. The first, GAP-1, appeared as a single band and was located anodally to the origin. GAP-2 was polymorphic for three alleles where the fast migrating homozygote was not apparent in the gel. The triple-banded heterozygous phenotypes observed for GAP-2, are typical of a dimetric enzyme.

Average Population Heterozygosity

There was a tendency for average heterozygosities to differ according to the geographic complexity of the system from which the different populations were collected. More complex systems had a higher average heterozygosity. The river population of *B aeneus*, for instance, had an average heterozygosity of 0,2659.

The effect of a less complex system on the average heterozygosity was most obvious in the population of *B. cf. kimberleyensis* with 0,2232. This population was isolated after the completion of the Hardap Dam in 1963. No new genetic material could therefore enter the dam by way of yearly spawning run. On the other hand, no spawning run takes place from the dam (Gaigher 1976), and this leads to a relatively small effective population size. The possibility of a genetic bottleneck in this population, that would result in a reduction of the gene pool, is therefore larger than the same happening for *B. aeneus*.

The average heterozygosity based on the electrophoretic data are 0,1200; 0,2395 for *L. capensis*, *L. umbratus* and the hybrid respectively. Comparing

these estimates with those of the Barrage namely, 0,1892 for *L. capensis* and 0,1698 for *L. umbratus* (Van Vuuren *et al.* in press), the same tendency that occurred in the *Barbus* populations was found here. The dam populations have a lower average population heterozygosity than those of the river populations, because of the isolation factor by the dam wall and the resulting smaller effective population size. As may be expected, the intermediate population of Hardap Dam has the highest average population heterozygosity (0,2395) of all five these populations. This high value for the average population heterozygosity, of this dam population, confirms thus the conjecture that this is in fact a hybrid between *L. capensis* and *L. umbratus*.

Genetic distance

The genetic distance between the samples for the *Barbus* species from the Barrage, is 0,1027 and between the "pure" *Labeo* samples from Hardap Dam 0,1317. However, it is of interest to note that the genetic distance between *B. cf. kimberleyensis* as well as *L. capensis* x *L. umbratus* are again intermediate to that of the respective pure populations (Table 8 and 9). This is a definite quantitative indication of hybridization between these species.

TABLE 8: Standard genetic distance (below diagonal) and standard deviations (above diagonal) between the respective *Barbus* populations from the Barrage and Hardap Dam.

	<i>B. aeneus</i>	<i>B. cf. kimberleyensis</i>	<i>B. kimberleyensis</i>
<i>B. aeneus</i>	—	0,0328	0,0752
<i>B. cf. kimberleyensis</i>	0,0408	—	0,0668
<i>B. kimberleyensis</i>	0,1027	0,0694	—

TABLE 9: Standard genetic distance (below diagonal) and standard deviations (above diagonal) between the respective *Labeo* populations from Hardap Dam.

	<i>L. capensis</i>	<i>L. capensis</i> x <i>L. umbratus</i>	<i>L. umbratus</i>
<i>L. capensis</i>	—	0,0194	0,0754
<i>L. capensis</i> x <i>L. umbratus</i>	0,0347	—	0,0188
<i>L. umbratus</i>	0,1317	0,0386	—

CONCLUSION

The results of this study prove unequivocally that morphometrical and meristical data alone are insufficient to distinguish between closely related species and their hybrids. This was clearly illustrated by the fact that some of the *Labeo* individuals, identified as either *L. umbratus* or *L. capensis* were indicated by electrophoretic results to hybrids.

The results also show that hybridization between fish species has occurred in Hardap Dam because of the disruption of biological cycles in fish populations and the construction of obstructions in rivers which prevent their natural movement. The *Barbus* population in this dam consists clearly of a hybrid population. *B. aeneus* and *B. kimberleyensis* are, however, quite closely related and more enzyme systems need to be analyzed before the taxonomic status of the Hardap Dam population can be proven beyond doubt. The third *Labeo* population is also a hybrid population and it is therefore of importance to identify natural, genetically pure populations as soon as possible, which can be conserved as breeding populations in the future.

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An electrophoretic and morphometric evaluation of the two subspecies of *Tilapia rendalli* from southern Africa

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ABSTRACT

Problems regarding the subspecific status of *Tilapia rendalli* (Boulenger 1896) and the lack of knowledge regarding the genetic status of these populations made it necessary to examine *T. rendalli* morphometrically and electrophoretically. Blood serum and muscle samples were respectively analysed on polyacrylamide and starch gels. Ten protein coding loci were analysed and no differences could be detected between the relative mobilities of the electrophoretic bands of the subspecies. Morphological differences as well as allele frequency differences and differences in genetic distance are inadequate for the division of *T. rendalli* into subspecies. It is therefore proposed that the subspecific status of *T. r. rendalli* (Boulenger 1896) and *T. r. swierstrae* (Gilchrist & Thompson 1917) be dropped.

INTRODUCTION

The current taxonomical criteria for the identification of tilapias is still mainly based on classical morphometrical analysis. In distinguishing between the two subspecies of *T. rendalli* (Boulenger 1896) morphometrical and meristical characters are however of limited use. It seems as though the only defining character between the two subspecies is the colour difference in the caudal fin (Trewavas 1980; Kenmuir 1983). According to these authors, the lower half of the anal fin for *T. r. rendalli* (Boulenger 1896) is red in colour and yellow in the case of *T. r. swierstrae* (Gilchrist & Thompson 1917).

The technique of gel electrophoresis of proteins provides a powerful tool in testing the validity of species, subspecies or strains. Because this technique allows the measurement of genetic affinity among individuals, it can serve as a means of identifying distinct species (Shaklee *et al.* 1982). Besides providing a method of species identification, the electrophoretic approach yields the additional benefit of determining the genetic structure of populations. Because of the difficulty to distinguish between the two subspecies of *T. rendalli* morphometrically, electrophoretic analyses were therefore conducted on these two subspecies.

MATERIAL AND METHODS

Sampling localities

T. r. rendalli individuals were randomly collected from the Upper Zambezi River near Katima Mulilo, South West Africa/Namibia. *T. r. swierstrae* were obtained from the Orlando Dam and the Olifants River, Transvaal, South Africa. Orlando Dam (situated near Johannesburg) is an isolated water body. Fish were collected during summer (December–April). Fifty or more individuals per locality were analysed.

Morphometrical and meristical measurements

These measurements were conducted using the standard techniques described by Lagler *et al.* (1977) and

Trewavas (1983). Total length, standard length, body depth, head length, head width, eye diameter, gill raker counts on the lower portion of the anterior arch, scale counts on the lateral line and dorsal and anal fin ray and spine counts were determined.

Electrophoresis

Blood was obtained from the dorsal aorta from each fish and the serum was separated by polyacrylamide gel electrophoresis. Blood serum samples were collected and prepared according to the methods described by Van der Bank and Ferreira (1987). Polyacrylamide gel preparation, electrophoresis and staining were conducted by the methods described by Avtalion and Wodjani (1971). Six percent polyacrylamide gels were used instead of the prescribed seven percent, since better resolution of serum transferrins were obtained. Polyacrylamide gels were stained for serum transferrins and esterases.

Starch gel electrophoresis was used for the analysis of proteins in muscle tissue. Approximately 1 g of white muscle was dissected from the thick layer of muscle under the dorsal fin. Muscle samples were homogenized and after fifteen minutes of centrifugation at 3 000 r.p.m. the clear supernatant was used for starch gel electrophoresis. The method of May *et al.* (1979) was applied in the electrophoresis using starch gels. The hydrolyzed potato starch that was used throughout the study was obtained from Sigma (S-4501). Thirteen percent gels were used. When the electrophoretic procedure was completed, gels were horizontally sliced and stained for lactate dehydrogenase (*LDH*), malate dehydrogenase (*MDH*), creatine kinase (*CK*) and 6-phosphogluconate dehydrogenase (*6-PGD*) according to the methods described by Harris and Hopkinson (1978). The different proteins, their enzyme commission numbers (E.C. no.) and buffers used are presented in Table 1.

Statistical procedures

The mean and standard deviation were determined for the morphometrical and meristical characteristics.

Using the G-test for goodness-of-fit, the deviations from Hardy-Weinberg proportions were determined. Expected heterozygosity (h), average heterozygosity (\bar{H}) and genetic distances were also calculated. These statistical analysis were carried out according to the methods described by Grant *et al.* (1980, 1983).

TABLE 1: The different proteins, their E.C. numbers and most suitable buffers in the electrophoretic analysis of *T. rendalli* samples.

Enzyme/protein	E.C. number	Buffer
CK	2.7.3.2	RW (Ridgeway <i>et al.</i> 1970)
LDH	1.1.1.27	MF (Market and Faulhaber 1965)
MDH	1.1.1.37	MF
6-PGD	1.1.1.44	TC (Whitt 1970)
Serum esterase	3.1.1.3	Tris-Glycine (Avtalion and Wodjani 1971)
Serum transferrins	-	Tris-Glycine

RESULTS AND DISCUSSIONS

Morphometrical and meristical data

The results for the three different populations are presented in Table 2. No significant differences ($P < 0.05$) were detected for HW/HL and dorsal and anal fin rays and spines. The Olifants River population showed higher mean values for ED/HW and HL/SL than the other two populations. This result can however be ascribed to the fact that all individuals sampled from the Olifants River were juveniles and it is known that these dimensions change with age (Moyle & Cech 1982). Although the mean values obtained for BD/SL, BD/TL, scale counts on the lateral line and gillraker counts different among the three populations, it still had overlapping ranges making it impossible to draw any firm conclusion. This result is, however, not unexpected for geographically separated populations (Van der Bank & Ferreira 1987) and it is also in agreement with the results obtained by Trewavas (1983).

The colour difference in the caudal fin of the two subspecies could not be detected. Both subspecies displayed yellow to red colours in the inferior part of the caudal fin. This characteristic could therefore not be used to distinguish between the two subspecies.

It is interesting to note that many authors refer to Trewavas (1966) for the subspecific division of *T. rendalli*. According to the British museum there are, however, no records for the subspecific division of *T. rendalli* (Trewavas pers. comm.). It is also important to note that although populations of the closely related *T. sparrmanii* also appear in these two geographically isolated regions, no attempt has been made to regard them as subspecies.

Electrophoretic loci

Creatine kinase (CK)

The CK bands only stained in RW-gels. The best

results were achieved with increased amounts of the compounds used in the staining procedure. Gels showed two zones after staining. All the populations were monomorphic for the CK-1 locus. Although heterozygotes usually result in three bands for dimeric enzymes, heterozygotes observed for CK possessed only double bands. This is probably due to temporal and spatial isolation (Ferris & Whitt 1978). Double bands were observed for heterozygotes of the Zambezi River, while the heterozygotes of the Orlando and Olifants Rivers possessed two to three bands. This deviation might be due to contamination during the preparation of the samples. The three banded state showed the familiar 1:2:1 banding intensity as expected for heterodimers. The electrophoretic bands possessed the same relative mobilities for the various populations.

Lactate dehydrogenase (LDH)

Muscle samples produced two LDH loci (LDH-A and LDH-B) and a single interlocus band after staining. The three populations were all monomorphic for both loci.

Malate dehydrogenase (MDH)

Two sitoplasmic loci (MDH-1 and MDH-2) were observed. A single mitochondrial locus (MDH-3) was occasionally present which showed one or two alleles. The sitoplasmic loci were monomorphic in all the populations.

6-Phosphogluconate dehydrogenase (6-PGD)

A single monomorphic locus was present in all the populations that did not differ in relative mobility.

Serum esterase (Est)

A single esterase locus was present in all the different populations. Observed allele frequencies met Hardy-Weinberg proportions. The only difference between the populations was found in the allele frequencies (Table 3).

Serum transferrins (Tf)

Three different transferrin alleles (A,B,C) were observed. Heterozygotes showed tripple or double bands and were in excess in all the populations (Table 3). Some of the genotypes presented low frequencies and were pooled in new classes. Due to the excess of heterozygotes, deviations of Hardy-Weinberg proportions were found for all the populations. The relative mobilities and allele frequencies of the transferrin bands did not differ significantly between the populations, making subspecies identification improbable.

Hardy-Weinberg proportions

Three (Tf, Est and CK-2) out of the ten loci examined were polymorphic. Tf and Ck-2 loci departed from expected Hardy-Weinberg proportions ($P < 0.05$). This is due to the excess of heterozygotes present at these loci. Values for the G-test are presented in Table 4.

Heterozygosity

The populations differ very little in average heterozygosity. The Orlando Dam population showed the highest \bar{H} value of 0,0860 ($\pm 0,0475$). A value of

TABLE 2: Morphometric and meristic characteristics of *T. r. rendalli* (Zambezi River) and *T. r. swierstrze* (Orlando Dam and Olifants River).

	Zambezi River (n = 50)			Orlando Dam (n = 50)			Olifants River (n = 25)		
	\bar{x}	Std-dev	Minimum Maximum	\bar{x}	Std-dev	Minimum Maximum	\bar{x}	Std-dev	Minimum Maximum
BD/SL	0,403	0,024	0,333 0,457	0,433	0,021	0,381 0,471	0,423	0,032	0,364 0,476
BD/TL	0,326	0,021	0,261 0,368	0,351	,019	0,313 0,395	0,339	0,02	0,304 0,375
HW/HL	1,048	0,221	0,452 1,3	1,082	0,111	0,857 1,375	1,023	0,044	0,931 1,10
ED/HL	0,238	0,040	0,164 0,422	0,24	,032	0,123 0,320	0,282	0,026	0,214 0,323
HL/SL	0,290	0,028	0,256 0,368	0,285	,019	0,242 0,333	0,324	0,016	0,292 0,361
SCALE COUNT	32,23	1,170	29,00 34,00	32,76	0,74	32,00 34,00	31,61	1,33	30,00 35,00
DORSAL SPINES	15,94	0,37	14,00 17,00	15,9	0,28	15,00 17,00	16,00	0,0	16,00 16,00
DORSAL RAYS	12,14	0,53	11,00 13,00	12,2	0,7	11,00 14,00	12,00	0,28	11,00 13,00
ANAL SPINES	3,00	0,0	3,00 3,00	3,00	0,0	3,00 3,0	3,00	0,0	3,00 3,00
ANAL RAYS	9,68	0,62	0,00 11,00	9,68	0,58	9,00 11,00	0,69	0,47	9,00 10,00
GILL RAKERS	12,50	0,99	10,00 15,00	13,06	0,77	11,00 15,00	13,57	0,9	12,00 15,00

BD = Body depth
 SL = Standard length
 TL = Total length
 HL = Head length
 HW = Head width
 ED = Eye diameter
 Scale count = Scale count along the lateral line
 Dorsal spines = Number of spines in dorsal fin
 Dorsal rays = Number of rays in dorsal fin
 Anal spines = Number of spines in anal fin
 Anal rays = Number of rays in anal fin
 Gill rakers = Number of gill rakers on anterior arch

TABLE 3: Allele frequencies of the proteins studied in the different populations of *T. rendalli*. Alleles are designated by their mobilities relative to the most common allele.

Species/locality	N	Protein/Enzyme loci	Allele frequency		
			A(80)	B(100)	C(120)
<i>T. r. rendalli</i> (Zambezi River)	52	CK-1	1,00	0,0	0,0
	49	CK-2	0,071	0,816	0,112
	52	LDH-1	1,0	0,00	0,0
	52	LDH-2	0,0	1,00	0,0
	52	MDH-1	1,00	0,0	0,0
	52	MDH-2	0,0	1,0	0,0
	52	MDH-3	0,0	0,0	1,00
	49	6-PGD	1,0	0,0	0,0
	49	Est	0,112	0,888	0,00
	51	Tf	0,304	0,412	0,284
<i>Tilapia r. swierstrae</i> (Orlando Dam)	52	CK-1	1,00	0,0	0,0
	52	CK-2	0,308	0,481	0,212
	52	LDH-1	1,0	0,0	0,00
	52	LDH-2	0,0	1,0	0,0
	52	MDH-1	1,00	0,0	0,0
	52	MDH-2	0,0	1,0	0,0
	52	MDH-3	0,0	0,0	1,0
	52	6-PGD	1,0	0,0	0,0
	37	Est	0,365	0,365	0,00
	51	Tf	0,255	0,255	0,490
	<i>T.r. swierstae</i> Olifants river)	26	CK-1	1,00	0,0
26		CK-2	0,2	0,5	0,3
26		LDH-1	1,0	0,0	0,0
26		LDH-2	0,0	1,0	0,0
26		MDH-1	1,00	0,0	0,0
26		MDH-2	0,0	0,0	1,0
26		MDH-3	0,0	1,0	0,0
26		6-PGD	1,0	0,0	0,0
26		Est	0,135	0,865	0,0
26		Tf	0,250	0,269	0,481

TABLE 4: Values of the G-test, the degrees of Freedom (F) and the Deficit of excess of heterozygotes (D), calculated for *T. rendalli*.

Population	Locus	G-Value	F	D
Zambezi River	Ck-2	4,085	3	0,1628
	Est	0,265	1	-0,0784
	Tf	7,6	1	0,2828
Orlando Dam	Ck-2	8,812	1	0,177
	Est	9,576	1	-0,1253
	Tf	30,01	1	0,495
Olifants River	Ck-2	12,476	1	0,4130
	Est	1,093	1	0,1556
	Tf	78,876	1	0,5776

0,0586 (+ 0,0344) was calculated for the Zambezi River population, and for the Olifants River population \bar{H} values of 0,0744 (\pm 0,0435) was obtained. The excess of heterozygotes present at the *Tf* locus of the Orlando Dam population, contributed to cause the high \bar{H} value of this proportion.

Genetic variation

The relative genetic variation within and between the different populations is presented in Table 5. It is obvi-

TABLE 5: The relative genetic variation within and between the different populations of *T. rendalli*.

Locus	Within populations	Between populations
Ck-1	0,0	0,0
Ck-2	0,959054	0,40946
LDH-1	0,818182	0,181818
LDH-2	0,0	0,0
MDH-1	0,0	0,0
MDH-2	0,0	0,0
6-PGD	0,0	0,0
Est	0,919643	0,080357
Tf	0,977612	0,022388
\bar{X}	0,958619	0,0438
Std-dev.	\pm 0,012414	\pm 0,012613

ous that there were less differences between the populations (4,4%) than between individuals of the same population (96%).

Genetic distance

The value obtained fall in the range of conspecific populations (Thorpe 1982). Although the Orlando Dam and Olifants River populations of *T. r. swierstrae* are genetically closer to each other, the differences between the three populations are insignificant causing their division into subspecies unnecessary. The genetic distance, standard errors and genetic identities are presented in Table 6.

TABLE 6: The genetic distance (Nei 1972) and standard error (below diagonal) and genetic identity (*I*) (above diagonal) for the different populations of *T. rendalli*.

	Z.R.	O.D.	O.R.
Z.R.	—	0,9903	0,9943
O.D.	0,0098 (\pm 0,0060)	—	0,9967
O.R.	0,057 (\pm 0,0045)	0,0033 (\pm 0,0029)	—

CONCLUSIONS

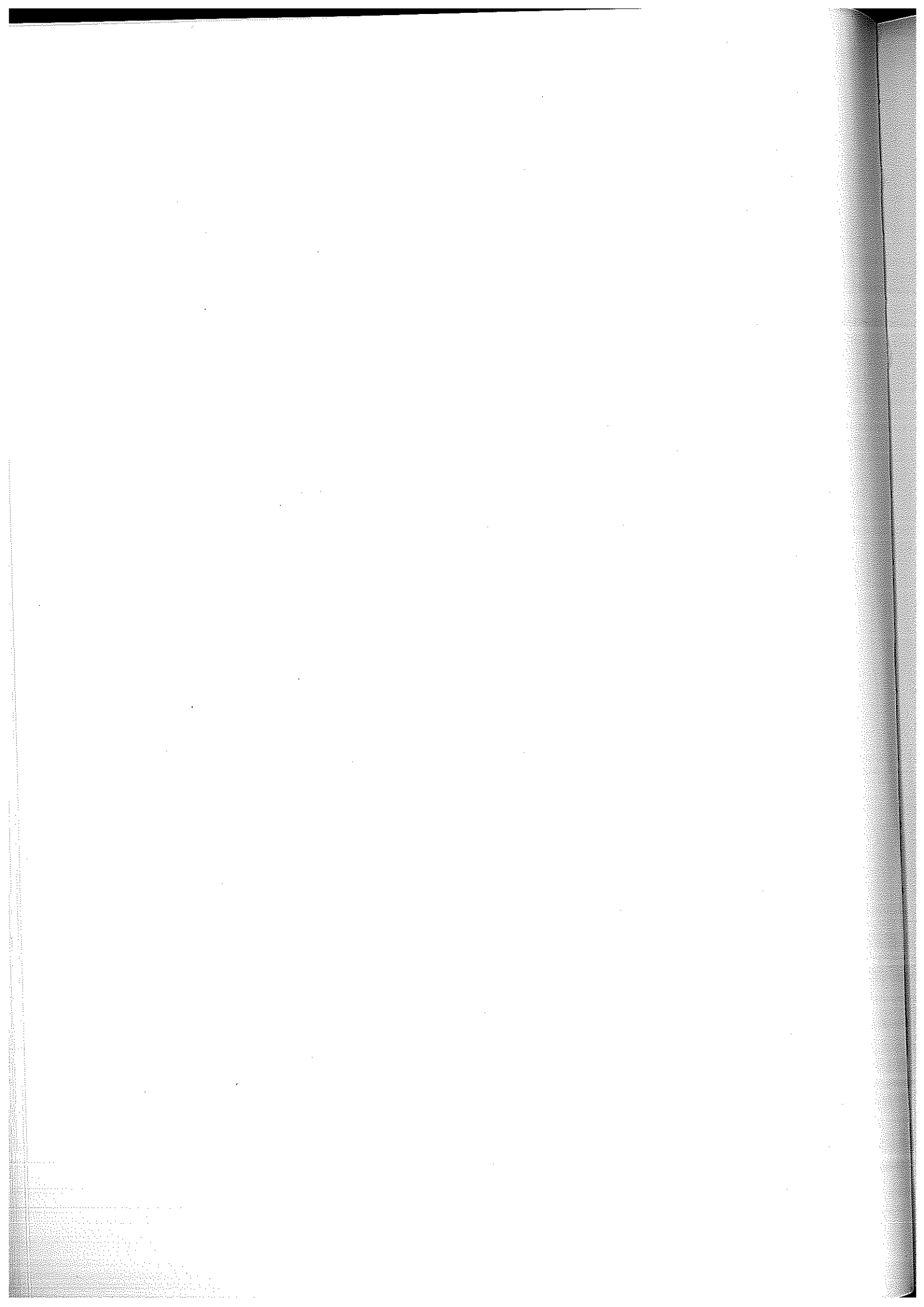
No colour, morphometric or electrophoretic differences could be detected between the subspecies of *T. rendalli*. Allele frequency differences and differences in genetic distance indicate conspecific populations and are therefore inadequate for the division of *T. rendalli* into subspecies.

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Biology of *Xerus princeps* (Rodentia, Sciuridae)

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ABSTRACT

The range of *X. princeps* is confined to a narrow band along the whole inland escarpment of SWA/Namibia, extending northwards into southern Angola. *X. princeps* are diurnal and reduce their exposure to high ambient temperatures through special behaviour (e.g. using the tail as a parasol). They live singly or in family groups of up to three (four?) animals. They dig simple burrows mainly among stones or rocks and feed on grass stems and roots. They also climb bushes to feed on plant lice. Some differences in habitat selection between *X. princeps* and *X. inauris* are described.

INTRODUCTION

Two species of ground squirrels of the genus *Xerus* occur in the southern African subregion: the Cape ground squirrel *X. inauris* and the mountain ground squirrel *X. princeps*. *X. inauris* is widely distributed in this region, whereas the range of *X. princeps* is confined to parts of the South West Arid biotic zone (see Davis 1962; Rautenbach 1978). While the biology and distribution of *X. inauris* has been studied in some details (eg. Smithers 1971; Herzig-Straschil 1978, 1979) no new information on life habits and distribution of *X. princeps* have been published since Shortridge (1934) and Roberts (1951) who characterized this species as an inhabitant of hilly and rocky and sometimes flat country in areas from Berseba north to southern Angola.

Recently, bioenergetics, thermoregulation and urin composition were studied on this species (Haim *et al.* 1987). In the present study we complete the distribution of *X. princeps* in the southern half of SWA/Namibia and discuss aspects of its biology.

MATERIAL AND METHODS

Observations on *X. princeps* were carried out in the summers of 1974, 1979 and 1985/86 in the Fish River valley, the Konkiep valley and Damaraland, all in SWA/Namibia. Binoculars (7×42) and a telescope (20×80) were used for the observations. A vehicle was used sometimes as a hide but in most cases rocks or the sparse vegetation had to suffice for this purpose.

Altogether 18 different individuals were observed for varying lengths of time. Since *X. princeps* are very similar to *X. inauris* in their general appearance it needs some experience to distinguish between them in the field. The most striking differences are the more bushy and longer tail and yellow incisors in *X. princeps* compared to a less bushy and shorter tail and white incisors in *X. inauris*. In some cases the field identification was verified by live trapping or the collection of a specimen.

Data from the literature, from museum specimens and field observations of the authors were combined to produce the distribution map.

One burrow was excavated completely. Temperatures (air and surface temperature in the sun, the shade and in burrows) were recorded in December 1985 using maximum-minimum thermometers in order to relate these to aspects of behavioural ecology.

RESULTS AND DISCUSSION

Distribution and habitat description

The distribution of *X. princeps* in SWA/Namibia is shown in Figure 1. It illustrates the additional localities documented by the present study which are situated south and southwest of Berseba (26° S), so far the southernmost localities published for *X. princeps* (de Graaf 1981; Smithers 1983). The localities further north are taken from the literature (Thomas 1929; Shortridge 1934; Roberts 1951; Hoesch & Lehmann 1956) supplemented by data from museum specimens (British Museum of Natural History, London; Kaffrarian Museum, King Williams Town; Transvaal Museum, Pretoria; Windhoek Museum, Windhoek). The range forms a narrow band along the whole inland escarpment of SWA/Namibia extending into southern Angola as far north as Mucungu (Hill & Carter 1941).

The main vegetation zones in which this species occurs are savannas and deserts (Giess 1971) and within these, mainly the Dwarf Shrub Savanna and Mopane Savanna as well as the Escarpment zone (the transition between semi-desert and savanna). Thus *X. princeps* inhabit areas with sparse ground cover where single trees or sparse bush may occur.

The average annual rainfall in these areas varies from below 125 mm to just above 250 mm (Schulze 1972). However, rain falls very irregular and long dry periods occur.

The ground substrate consists of gravel and rocks; only once was *X. princeps* found on more sandy soil.

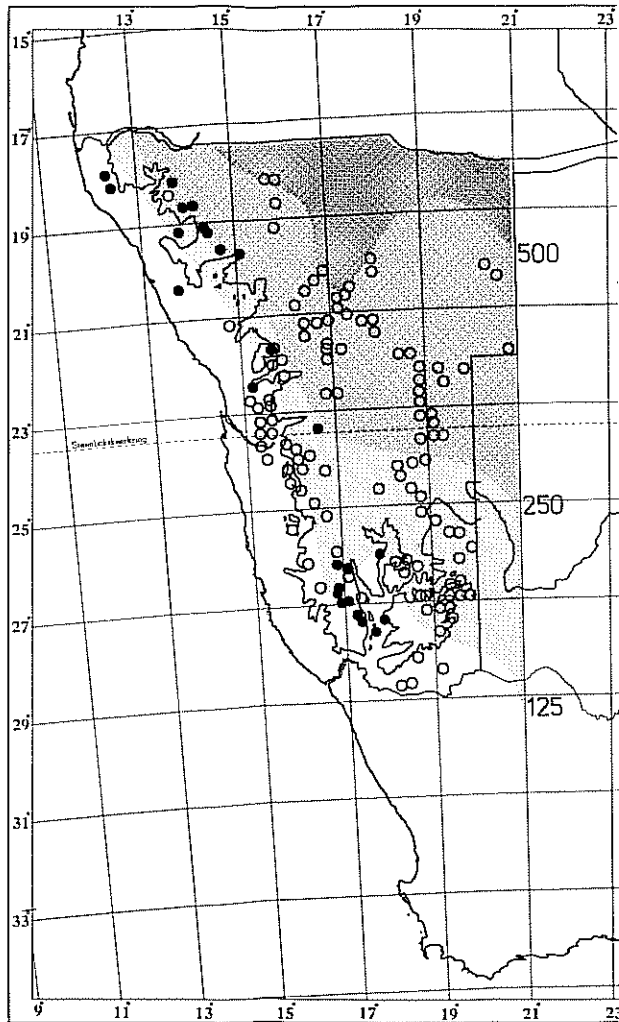


FIGURE 1: Distribution of *Xerus princeps* (●) and *Xerus inauris* (○) in SWA/Namibia. Inland solid line marks 1000 m altitude. Areas of different average annual rainfall (mm) are indicated by shading (see text for details).

The rocks are mainly granite but areas with limestone were also inhabited (Plate 1–4).

Daily activity, behavioural thermo-regulation

X. princeps are strictly diurnal and spend the nights in burrows. During normal sunny days in summer they become active above ground between 06h55 and 07h50 and retired to the burrow between 18h05 and 19h15. Unfavourable weather (heavy rain, exceptional heat) usually alter these times causing them to leave the burrow later or alternatively, return to it earlier. This was observed on two windy days when temperature exceeded 55°C in the late morning (Fish River valley 1979) and virtually no shade occurred in the vicinity; the ground squirrels returned to their burrows before mid-day and only a few of them reappeared in the afternoon.

On emerging in the morning squirrels sat in the sun for a short while and self-groomed. They started feeding and left the vicinity of the burrow within 10 to 15 minutes. No allogrooming or playing was observed

among burrow mates. Most of the day was spent away from their burrows feeding. Animals were seen at distances of up to 1 km from their burrow.

In the evening, on returning to the burrow, they either entered it immediately or briefly paused in the vicinity of the tunnel opening to inspect the surroundings and sometimes groomed themselves.

In the morning when emerging from the burrow the squirrels sometimes showed signs of hypothermia (hair erection) and sat in the sun. During the heat of the day the animals used their long tails as portable parasols (Figure 2). This behaviour has been described for *X. inauris* (Smither 1971; Marsh *et al.* 1978; Herzig-Straschil 1978, 1979). Bennet *et al.* (1984) cor-

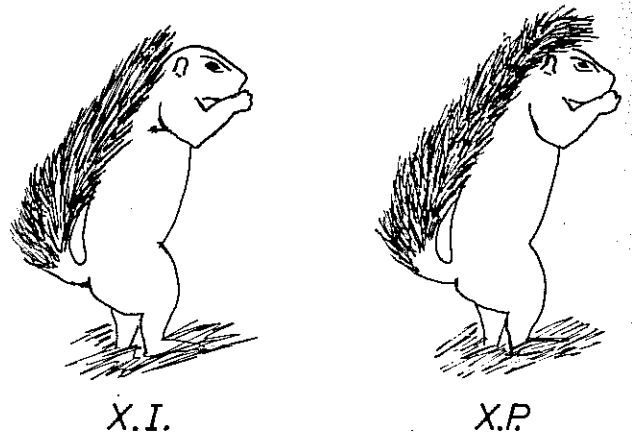


FIGURE 2: *Xerus inauris* (X.i) and *Xerus princeps* (X.p.) using their tail as a parasol.

related this behaviour with environmental heat load and showed its use doubled the animals time for foraging. *X. princeps* has a longer tail than *X. inauris* (Analysis of the data from Figure 3: Mean tail length [mm] *X. princeps* – 245,4 ± 19,2 [S.D.]; *X. inauris* – 210.6 ± 15,3 [S.D.]; One Factor Anova reveal a significant difference at 95 %) which results in a more effec-

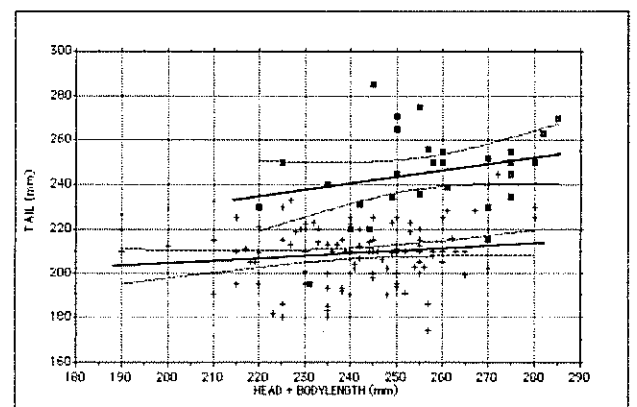


FIGURE 3: Relationship between head & bodylength and the length of the tail for *Xerus princeps* (■) and *Xerus inauris* (+). Regression lines and 95 % confidence intervals are indicated.

Regression equations: *X. princeps*: $y = 0.294 + 170.31$

X. inauris: $y = 0.118 + 180.53$

(Pooled data from museum specimens collected S. M.S.P. 14 by M. Haupt [MRI] and the authors)

tive shading of the body and the head (Figures 2 & 3). When the sun was standing high *X. princeps* often kept in the shade of bushes, trees or rocks (Plate 4) and hurried across the exposed areas in between. Temperature measurements taken in such areas in December 1985 are given in Figure 4. It is apparent that air temperatures in the shade were 5°–12° C below those in the sun ($\bar{x} = 37.5^\circ\text{C}$) during the heat of the day. It

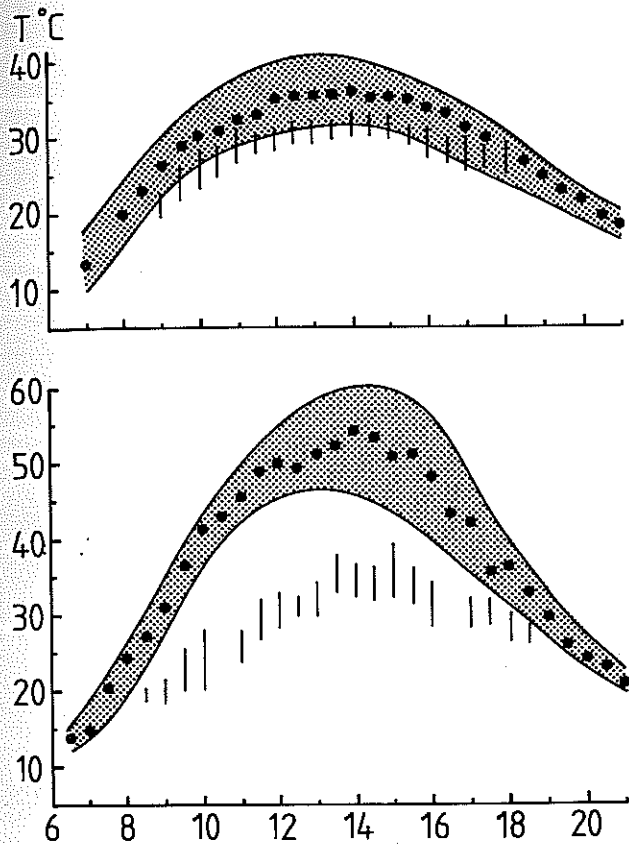


FIGURE 4: Temperature measurements (18.–22. December 1985); Top: Air temperature; Bottom: Ground surface temperature; Shading: Temperature range in the sun (● mean T° C); Vertical lines: Temperature range in the shade

is also apparent from this figure that the ground surface temperatures differ by up to 20° C between shaded and exposed areas. These pronounced differences in temperatures are reflected in the behaviour of *X. princeps* which used all means to reduce the heat load and sought shade during activity.

Burrows

Burrows were sometimes situated on a gravel plain but more often they were found under piled up stones or underneath rocks which formed the roof of the tunnel openings. When there are no suitable natural rocks available they burrowed under concrete platforms at waterpumps (Konkiep valley) or piled up stones used in road works (northern Damaraland). In front of the burrow openings was usually a low mound of material that was dug out of the tunnel.

A single burrow inhabited by three individuals (1 adult ♀, 1 subadult ♀, 1 subadult ♂) was excavated in gravel

soil at the Erongo mountains in January 1986. It consisted of a single central nest chamber with two tunnels to the surface (Figure 5). The chamber contained no real nesting material but only an old brittle plastic bag which was half covered by earth. No parasites were found in the burrow; the bottom of the nest chamber was 67 cm below ground surface.

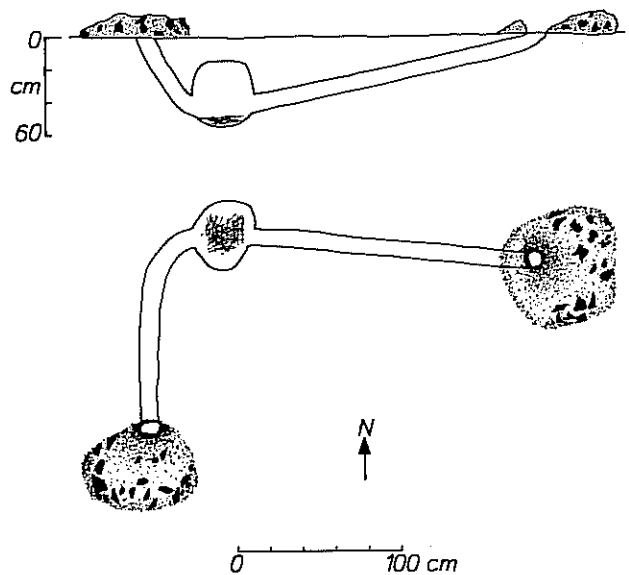


FIGURE 5: Burrow of *Xerus princeps* (Farm Davib Oos, SWA/Namibia)

Inspections of other burrows (as far as was possible under stones and rocks) never implied a much more complicated structure than the one illustrated in Figure 5 apart from a varying number of openings to the surface (from two to five).

The distance between inhabited burrows was at least 80 m (Fish River valley 1974) but usually they were more than 100 m apart. Recordings of air temperature inside and outside burrows were taken in December 1985. The mean values inside the burrows varied between 24.6° C (night) and 31.5° C (day) and were well above the mean minimum night temperature of 9.7° C and below the mean maximum day temperature of 37.5° C outside (Table 1).

TABLE 1: Mean air temperature inside *X. princeps* burrows and outside (18th–22nd December 1985)

cm inside burrow	cm below surface	mean T° C min (night)	max (day)
90–100	27	$\bar{x} = 25.7$ n = 4 (24–27)	$\bar{x} = 31.5$ n = 4 (31–32)
60–70	30–50	$\bar{x} = 24.6$ n = 3 (24.5–25.5)	$\bar{x} = 30.6$ n = 3 (30–32)
outside		$\bar{x} = 9.7$ n = 6 (7–12.5)	$\bar{x} = 37.5$ n = 4 (35–38)

n = Number of recordings, two different burrows

Social structure and reproduction

X. princeps might live singly, in pairs or in family groups consisting of an adult female and her subadult offspring. Table 2 summarizes group sizes observed by the authors and by M. Haupt (pers. comm.)

TABLE 2: Groups of *X. princeps* inhabiting one burrow

ad♂♂	sad♂♂	ad♀♀	sad♀♀	Total	month
—	1	1	1	3	July/August
1	—	2?	—	3	July/August
—	—	1?	—	1	July/August
2 or 1 or 1?	2	—	—	2	July/August
—	1	—	—	1	July/August
1?	—	1	—	2	November
—	2?	1	1?	4	November
—	1	1	1	3	Nov./Dec.
—	1	1	1	3	January

ad = sexually mature; sad = sexually immature but older than about 8 weeks

Field identification: ad♂ large scrotal testes; sad♂ no well visible testes ad♀ clearly visible mammae; sad♀ minute mammae

One female *X. princeps* gave birth to a single male young after being kept isolated for 48 days. This indicates a gestation period similar to that reported for *X. inauris* of 42–49 days (Zumpt 1970). The eyes of the young opened after 21 days (M. Haupt pers. comm.). The litter size observed in the field varied from 1–3 (9 observations). No young (younger than about 8 weeks) were seen during the summer month.

Food and feeding habits

X. princeps fed mainly on the ground on the base of grass stems or on grass roots. They feed in typical squirrel-like manner picking up food items by mouth and handling them with the forepaws.

In the mopane savanna in northern Damaraland two specimens were observed feeding for 35 minutes on plant lice and their wax cover on *Colophospermum mopane* leaves. To reach more of this apparently favoured food they climbed first the strong bottom branches of a mopane bush. One climbed to a height of 2 m above ground where the main branches were only about 2 cm thick. While foraging there in squirrel-like manner it frequently sat in the fork of a branch on its haunches but often also lost its balance when reaching out for distant leaves. The long tail seemed to assist in regaining or maintaining balance (Plate 5). *X. princeps* thus cannot be regarded as purely a ground feeder although this was the only such observation throughout the study period.

Flight distance and flight behaviour

When disturbed during its daily activity in the field *X. princeps* hid behind rocks or under bushes and would leave this shelter only when forced to do so by the proximity of the persuer (usually about 5–9 m, exceptionally 1 m only). Then it would make for another shelter some distance away and would wait there if

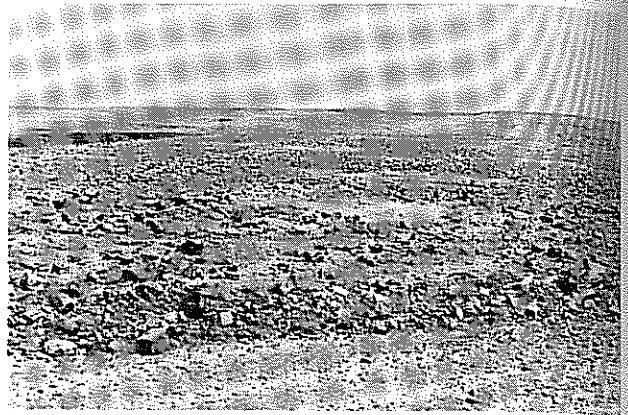


PLATE 1: *Xerus princeps* habitat at Fish River Canyon



PLATE 2: *Xerus princeps* burrow entrance; habitat Konkiep Valley

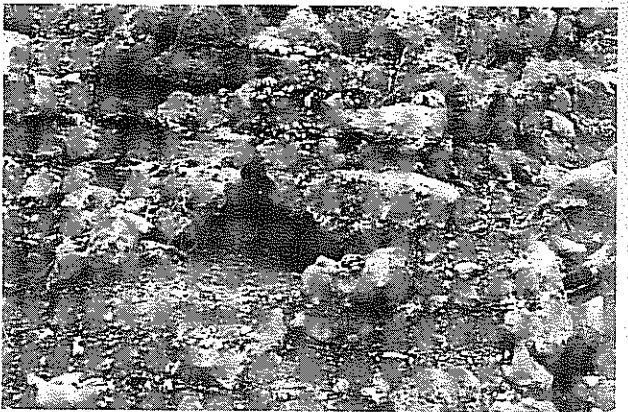


PLATE 3: *Xerus princeps* burrow entrance; habitat Damaraland

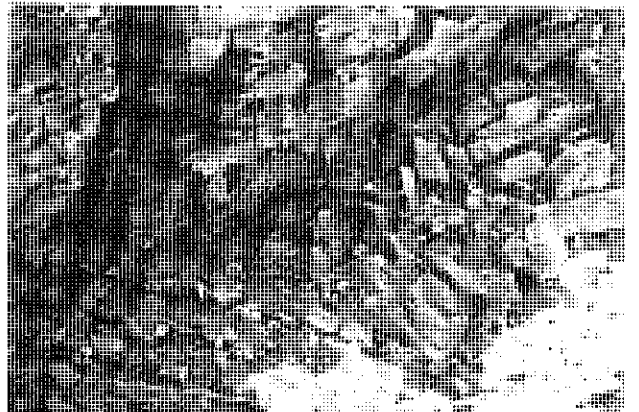


PLATE 4: *Xerus princeps* resting in the shade; habitat Fish River Canyon



PLATE 5: *Xerus princeps* feeding in a Mopane bush

persued further. On one occasion it took some minutes to induce a *X. princeps* to vacate a dense milk bush and run further. Although they seem to flee in the direction of the burrow they were not seen to enter the burrow directly as a means of escape as often happens in *X. inauris*.

CONCLUDING REMARKS

Intensive field observations on *X. princeps* were difficult because of a low population density in certain areas and the rugged habitat they occupied.

The distribution map shows some sympatry between the ranges of *X. princeps* and *X. inauris* but although both were found within a few hundred metres in the area around the Erongo mountains no local interaction was observed. The two species are separated with respect to habitat selection, social behaviour and structure of their burrows (Table 3) but the mechanisms which keep them separated when living only 200 m apart (Haim *et al.* 1978) cannot be defined and re-

TABLE 3: Obvious differences in habitat and life habits of *X. princeps* and *X. inauris*

	<i>X. princeps</i>	<i>X. inauris</i>
habitat	mountains, kopjies, rarely flats; rocks, stones, gravel, rarely sand; sparse vegetation only (grass, bushes)	flat country; sandy, calcareous substrate; sparse to closed; grasscover, bushes, isolated trees
burrow	simple, 2-5 openings	complicated burrow-systems, 2->100 openings
number of inhabitants per burrow	1-4	1-14 (up to 3 such groups in extensive burrow systems)
social organization	single, pairs or female with offspring; no colonies	rarely single; forming colonies
social contacts	almost none, rarely one might sniff at the other	regular among group members (allogrooming, playing etc.)

main as yet another interesting topic for further studies on this species.

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Range extensions, food and breeding of the Marsh Owl in the northwestern Namib, South West Africa/Namibia

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ABSTRACT

Marsh owls *Asio capensis* were found at 13 localities along the northwestern Namib, SWA/Namibia. Three nests were found. These records indicate a more extensive distribution along the Namib coast than was previously thought. Observations were made on the owl's hunting methods, food, breeding biology and behaviour near the nest.

INTRODUCTION

The marsh owl *Asio capensis* is an African species thought previously to occur only in open, grassy and marshy habitats (Mackworth-Praed & Grant 1962). Although Steyn (1982, ex. Dixon 1970) refers to isolated pockets in the west of SWA/Namibia, Newman (1984) and Maclean (1985) give no distribution for this area.

This paper reports on new distribution and breeding records within and adjacent to the Skeleton Coast Park, in northwestern SWA/Namibia.

STUDY AREA AND METHODS

Observations were made on the breeding behaviour of marsh owls in the Ugab River mouth (21° 09'S; 13° 40'E) and the Uniab Delta (20° 10'S; 13° 13'E) in the Skeleton Coast Park, and the Obob River in Damaraland (19° 53'S; 13° 27'E). The first two sites were in dense scrub, surrounded by open gravel plains and fluvial terraces. The third site was in eroded gullies surrounded by open gravel and stony plains.

Daily observations were made on the Ugab nest from when it was first located on 9 April (containing three eggs) until the nestlings had left the nest on 9 May. The Uniab nest site, also found in April (with two eggs), was visited infrequently until the nest was deserted. The Obob nest (with two nestlings), found on a patrol in mid-June, was not revisited. The Ugab nest was visited every afternoon, usually between 17h00 and sunset at about 20h00. Pellets were collected and identified by Dr. M. Avery of the South African Museum, Cape Town. Remains of fresh prey brought to the nest were identified when possible, but invertebrate prey was under-represented in these samples.

RESULTS AND DISCUSSION

Distribution

Sight and breeding records for marsh owls along the northwestern Namib coast (Figure 1) indicate that they are confined mainly to river courses and particularly to the delta regions of rivers, but they were also seen away from rivers in the desert. These latter sites are considerably more arid than the habitat previously

ascribed to this species (e.g. Steyn 1982). These birds probably return to the river courses during dry periods and to breed.

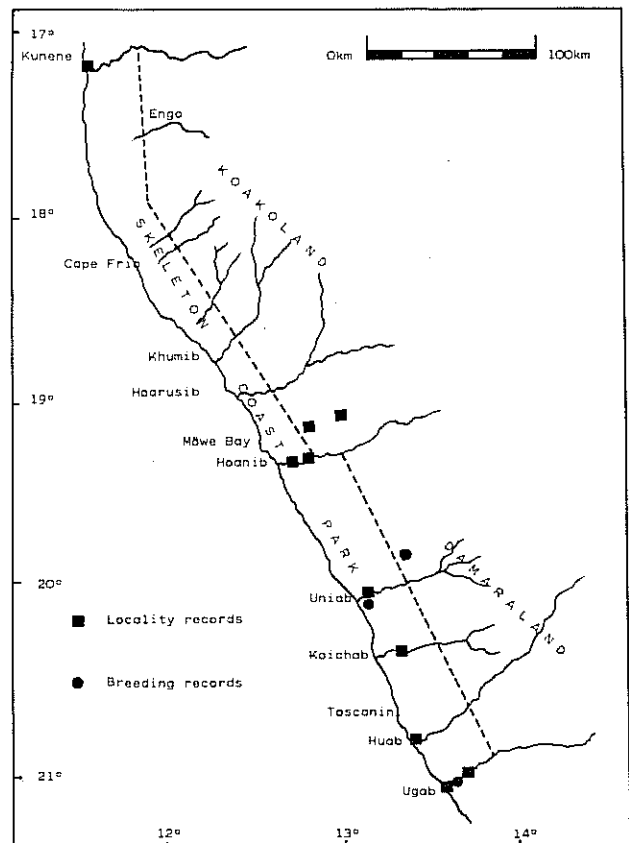


FIGURE 1: Sight and breeding records for marsh owls along the northwestern Namib Coast.

Hunting methods

The hunting methods recorded were similar to those documented by Steyn (1982). The owls either hunted from a perch or while in flight. When hunting from a perch the Ugab owls would sit motionless on the outer branches of a dried out *Nicotiana glauca* or *Acacia al-bida* overlooking the river bed, which was vegetated mainly by grass and sedges. After spotting prey, the owl would glide towards the area and then drop onto the prey with talons outstretched and wings arched upwards. The average time spent perch-hunting between

attempted strikes was 1,5 min ($n = 6$). The percentage of successful hunts could not be assessed because of the high vegetation. When hunting on the wing the owls would glide slowly over the ground at 1–2 m above the vegetation. On locating prey, the owl would dive into the grass, and disappear from sight. Sometimes the owls would hunt from 3–4 m above the vegetation, hovering over an area for about 6 s before resuming the quartering flight. Strikes at prey were sometimes also made from a hovering position. The average time spent gliding and hovering between perching was 4 min 45 s ($n = 9$). The Uniab owls did all their hunting from the wing as there were no suitable perches in the area.

Prey

A list of prey items ($n = 351$) identified from pellets is given in Table 1. Nine fresh prey items brought to the nest consisted of *Parotamys littledalei* ($n = 5$), *Rhabdomys pumilio* ($n = 3$) and a Cape sparrow *Passer melanurus*. Of the total sample, 86% (by number) were small mammals, 0,3% birds and 14% invertebrates, mainly insects. By mass, approximately 97% was of small mammals, mainly rodents. This is similar to the findings in other collections of marsh owl pellets, where rodents and insects predominate (Steyn 1982).

TABLE 1: Diet of the marsh owl in the Skeleton Coast Park, determined from pellets collected from two nest sites in the Ugab and Uniab Rivers. The data on the mammalian prey remains were published previously by Avery (1986).

Group	Species	No. records	
Mammals: Insectivora Rodentia	<i>Crociodura cyanea</i>	4	
	<i>Desmodillus auricularis</i>	4	
	<i>Gerbillurus paeba</i>	230	
	<i>Praomys natalensis</i>	45	
	<i>Rhabdomys pumilio</i>	7	
	<i>Parotomys littledalei</i>	7	
	<i>Petromyscus collinus</i>	3	
	Subtotal (mammals)	300	
Insects: Scarabidae	<i>Scarabaeus</i> sp.	10	
	<i>Heteroliqus peringueyi</i>	6	
	Tenebrionidae	<i>Cauricara brunhipes</i>	1
		<i>Onymacris bicolor</i>	1
		Unidentified sp.	4
	Cuculionidae	<i>Cleonus</i> sp.	4
		Unidentified sp.	1
	Orthoptera	<i>Comicus</i> sp.	3
		Unidentified crickets	9
		Unidentified grasshopper	2
Arachnids:	<i>Carparachne</i> sp.	8	
	Unidentified solifuge sp.	2	
	Subtotal (invertebrates)	51	
Total		351	

Nest sites

The nest sites chosen by the owls differed at the three localities. The Ugab nest was amongst dense *Sueda*

plumosa scrub and *Sporobolus virginicus* grass, surrounded by *A. albida* and the invasive alien *N. glauca* which were used as perches. The Uniab nest was well hidden under large (1,5 m tall) *Scirpus diocus* sedge with no higher vegetation nearby to offer perches. The Obob nest was on top of a rock shelf under the matted inner branches and roots of a *Salvadora persica* growing against a rock face in the river.

Both the Ugab and Uniab nests were typical of the species, being well hidden and with a short tunnel entrance consisting of a shallow basin of matted dry grass. The Obob nest was atypical; it was not well hidden and the nest basin was flat and built on top of a rock shelf. The Ugab and Uniab nests were near the coast, and both had northwest facing entrances. The prevailing wind along the coast is southwest and many birds build their nests facing north in this region, e.g. dusky sunbirds *Nectarinia fusca* (per. obs.)

Breeding period

Two nests were found in April, containing two and three eggs respectively. The mean measurements of the five eggs were $39,7 \times 33,8$ mm (range 38,7 – 40,2 \times 33,1 – 34,3 mm) which compares favourably with published measurements (Steyn 1982; Maclean 1985). The other nest, found in mid-June, had two nestlings. The first egg in the Ugab nest hatched on 20 April and by 24 April all three eggs had hatched. Taking the incubation period as 27–28 days (Steyn 1982) the eggs were laid on about 22–25 March. These records coincide with the March–April laying peak suggested by Steyn (1982).

Parental and nesting behaviour

The Ugab nest was found when one of the adults was flushed from underfoot and circled overhead before landing again. On subsequent visits the owl flew overhead and occasionally uttered a harsh croak. This sometimes attracted its mate, which also flew about, but did not call. Once the observer had moved about 40 m away the owl settled and continued incubating. This behaviour continued until the eggs hatched, when the bird became more agitated and aggressive. The bird would mock-dive an intruder and call constantly. The mate also called during this period. When the nestlings were about 10 days old the owl on duty at the nest would fly up when an intruder was 50–70 m away and start diving and calling. When the nestlings were about 14 days old the parents began "broken wing" distraction displays. These were done in the vicinity of the nest while emitting high-pitched mewing calls. The parent birds would flop across the grass, moving away from the nest, for 30–40 m before flying off and settling 60–80 m away. Similar behaviour was recorded by Dean (1969) and Steyn (1982). At about 12 days old nestling were sitting upright, hissing and snapping their bills at the observer. This continued until the nestlings left the nest, on 9 May, at about 20 days old (cf. Steyn (1982) states that the

nestling can stand at 10 days and leaves the nest at 18 days). After the nestling had left the nest, the parents continued performing the broken wing displays as well as circling and croaking above the intruder when he approached to within about 50 m of the young owls.

One of the adult birds, probably the female, played a major role in the incubation and care of the nestlings. Alarm and distraction displays were initiated by this bird. The other parent usually roosted in the sedge and grass about 100 m away, and would join the on-duty bird only once it had started to call.

Two of the three breeding records were successful, producing five young (1.7 per breeding attempt). These records suggest a more resident population on the northwest Namib coast than was previously thought. Steyn (1982) suggests that "although stated to be resident, this species is undoubtedly nomadic to a certain extent". This is probably true, but at some localities, e.g. some rivers and deltas which remain well vegetated throughout the year as well as in dry years, the birds may well be resident.

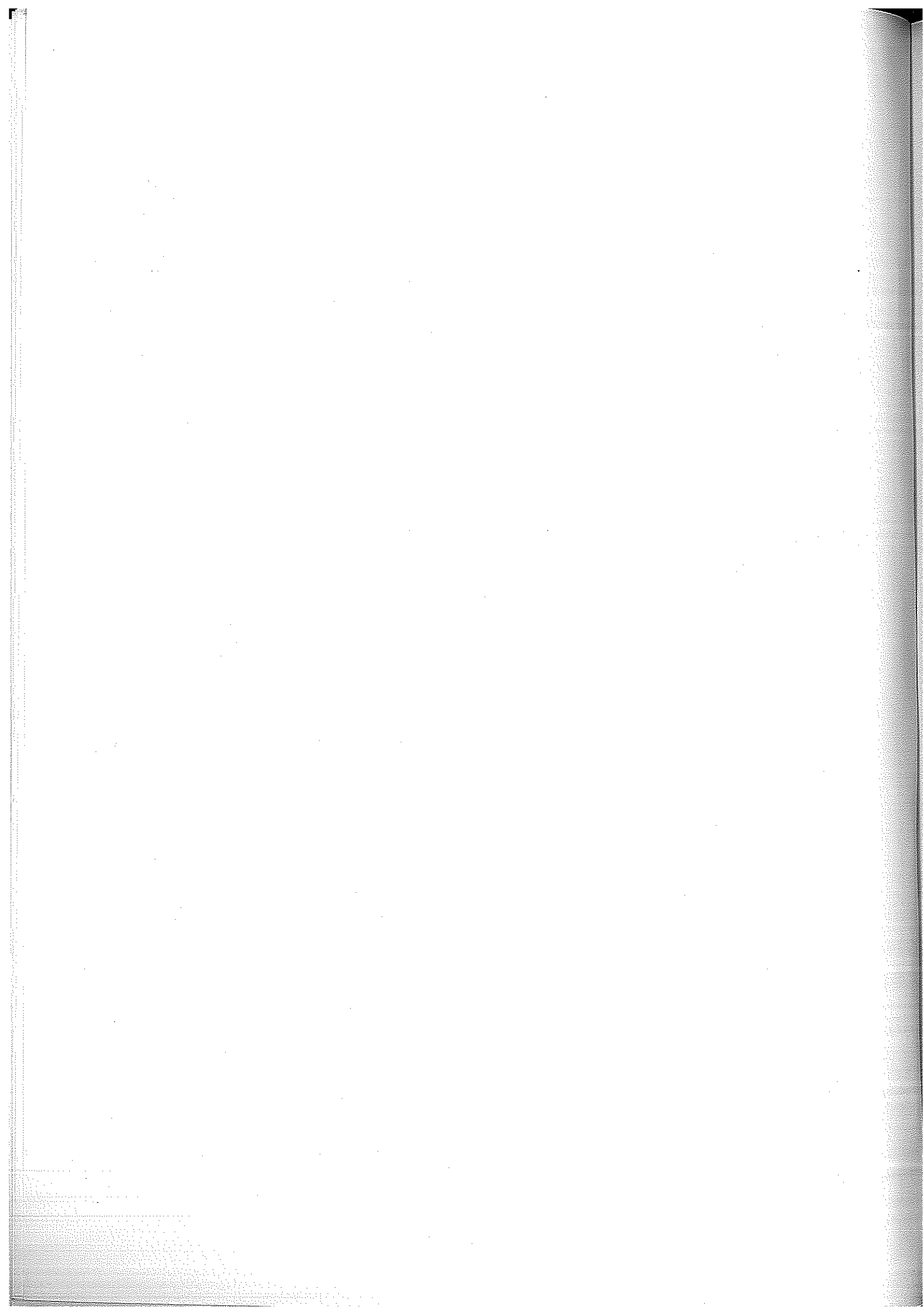
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The status of alien invasive plants in the major rivers of the Namib Naukluft Park

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ABSTRACT

The major rivers of the Namib Naukluft Park were surveyed to determine the degree of infestation of alien invasive plants. The Swakop and Kuiseb Rivers had the densest infestations, the Tsondab and Tsauchab Rivers had less dense infestations, while no alien plants were found in the Awasis and Koichab Rivers. *Datura innoxia* and *Nicotiana glauca* were the most abundant alien plant species.

While it may not be possible to eradicate *D. innoxia*, an ephemeral species, using mechanical methods, it is suggested that this species may have little impact on the indigenous vegetation and therefore is of less importance than the perennial alien species. The perennial species, *Prosopis* spp., *N. glauca* and *Ricinus communis* appear to have a greater impact on indigenous vegetation than the ephemeral species and priority should be given to their control.

INTRODUCTION

Conservation of biotic diversity is one of the main aims of nature conservation authorities. The existence of alien invasive species within natural parks poses a threat to indigenous communities.

Invasive alien plant species have been introduced to southern Africa both directly and inadvertently, often as seeds in imported fodder (Brown & Gubb 1986). Some species have now spread throughout much of South West Africa/Namibia, colonizing, in particular, areas which have been disturbed either by man's activities or through natural causes.

At present little is known of the distribution, density or competitive abilities of alien invasive species in the Namib Desert. This paper is intended to provide a synopsis of the occurrence of these species, and their levels of infestation, within the major river systems in the Namib Naukluft Park.

METHODS

The major rivers of the Namib Naukluft Park (Figure 1) were surveyed using the river transect method developed by the South African Botanical Research Institute (Henderson & Musil 1984). The method used was to record alien plants from a slow moving vehicle, travelling, with the exception of a small section of the Koichab River, in the centre of the riverbed. All rivers were surveyed from west to east.

Three rivers, the Tsondab, Tsauchab and the eastern 75 km of the Kuiseb River were surveyed during December 1987. These rivers had all last flowed at the beginning of 1987. The Koichab and Awasis Rivers, which apart from some local run-off had not flowed for a number of years, were surveyed in February 1988. The western section of the Kuiseb River, a 54 km-section downstream of Gobabeb, and the Swakop River were surveyed in April 1988, three months after they had last flowed.

The Swakop River was surveyed from the western boundary of the park to the eastern boundary, a distance of 86 km. The Kuiseb was surveyed from the western park boundary to the point where vehicular travel is no longer possible (129 km).

The Tsauchab and Tsondab Rivers were surveyed from their vleis to the eastern boundary of the park (70 and 49 km respectively). The small loop of the Tsauchab River outside the park was not surveyed.

The Awasis River was surveyed from a point about 5 km east of the Awasis Pan to the eastern park boundary; a total distance of 16 km.

The Koichab Depression (20 km) and western section of the Koichab River (21 km) were surveyed from tracks alongside the watercourse. The river was surveyed in the water course from the main Water Affairs pumping station eastwards to the park boundary (63 km).

Abundance and frequency ratings were recorded for each 1 km of river traversed and these are reported as mean ratings for sections of the river. Each section was normally 10 km in length except for the last section of each river. Vleis were reported separately. Abundance ratings were those used by Macdonald & Nott (1987) and are summarized in Table 1.

TABLE 1: Abundance ratings used for surveying alien plant species in rivers (from Macdonald & Nott 1987).

RATING	DEFINITION
9	Species forming a virtually continuous, almost monospecific stand at least 1 ha in extent.
8	Species co-dominant in a virtually continuous stand at least 1 ha in extent.
7	20 or more plants per 1 km-section
6	10-19 plants per 1 km-section
5	5-9 plants per 1 km-section
4	2-4 plants per 1 km-section
3	1 plant per 1 km-section

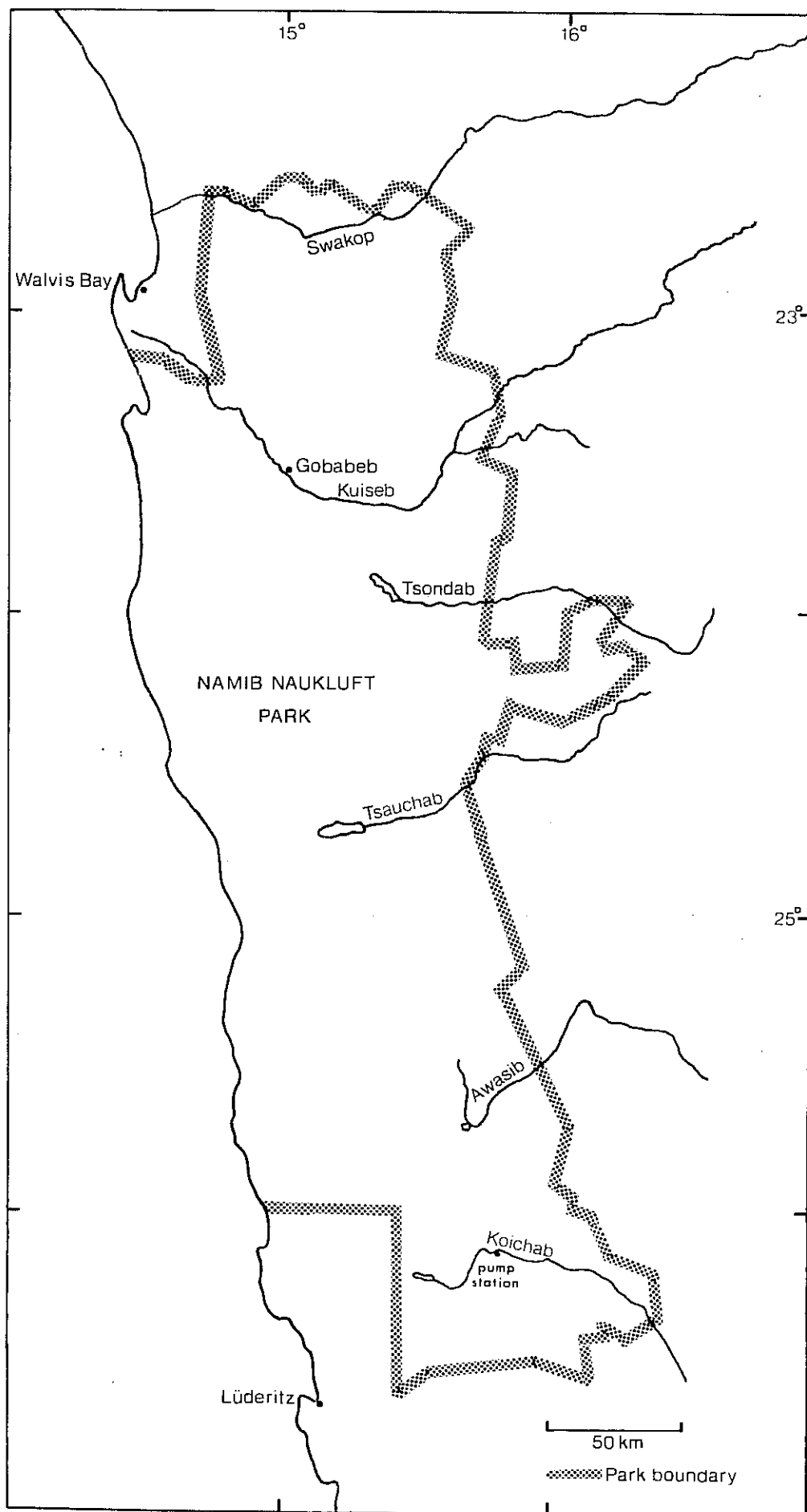


FIGURE 1: The six major rivers of the Namib Naukluft Park.

Mean abundance ratings (A) were then calculated for each species within each 10 km-section of each river, using the formula:

$$A_z = \frac{\text{Sum of 1 km abundance ratings of species Z/section}}{\text{Number of 1 km-sections having species Z}}$$

Two frequency ratings were calculated. The frequency of occurrence (F_o) is the percentage of 1 km-sections within which a species was found to occur, and was calculated as follows:

$$F_o(z) = \frac{\text{No. of 1 km-sections in which species Z occurred}}{\text{Number of km traversed (normally 10)}} \times 100$$

To give an indication of the management implications involved in controlling each species a rate of frequency of occurrence of dense infestations (F_i) was calculated. A dense infestation was taken as any section with an abundance rating of 5 or greater (more than 20 plants per 1 km traversed) of that particular species.

This was calculated using the formula:

$$F_i(z) = \frac{\text{No of 1 km-sections where } A_z > 4}{\text{Number km traversed (normally 10)}} \times 100$$

All original data are stored at the Namib Research Institute, Namib Naukluft Park.

RESULTS

The genus *Prosopis* is currently under revision and specific names cannot be given with any confidence. The species found in the Namib are therefore referred to as *Prosopis* spp.

Swakop River

This river had the most alien invasive species of all the rivers surveyed, a total of six species (Tables 2 & 3), i.e. *Argemone ochroleuca* Sweet (Mexican Thistle), *Nicotiana glauca* R.C. Graham (Wild Tobacco), *Ricinus communis* L. (Castor Oil Bush), *Datura innoxia* Mill. (White Thorn Apple), *D. stramonium* L. (Purple Thorn Apple) and *Prosopis* spp. (Mesquite).

D. innoxia had the greatest abundance rating and occurred more frequently than the other species. Except for the upper 20 km of the river, this species occurred throughout at a rate of more than 20 plants/km. *D. stramonium* and *Prosopis* spp. also occurred less frequently in the upper region. *N. glauca* was found throughout the river, with dense infestations in about one third of all the 1 km-sections. While *R. communis* was found throughout the river, it only occurred at low densities. *A. ochroleuca* was rarely seen.

Twenty-one palm trees (*Borassus aethiopum* and *Phoenix reclinata*) were recorded. While these species are probably non-invasive in the Namib, they are, however, alien to this region.

Kuiseb River

Five alien species were detected in this river (Tables 4 & 5). *N. glauca* and *D. innoxia* were found in most of the 1 km-sections (Tables 6 & 7), and occurred more densely than any of the other alien species. *A. ochroleuca* and *R. communis* occurred most frequent-

TABLE 2: The abundance ratings (A) of alien plants in the section of the Swakop River within the Namib Naukluft Park.

Distance from west (km)	<i>Argemone ochroleuca</i>	<i>Datura innoxia</i>	<i>Datura stramonium</i>	<i>Nicotiana glauca</i>	<i>Prosopis</i> spp.	<i>Ricinus communis</i>
0-10	—	7,0	5,4	5,2	6,6	4,8
11-20	—	7,0	5,6	6,0	6,6	4,3
21-30	3,0	7,0	5,3	6,0	6,7	3,3
31-40	—	7,0	5,2	6,5	6,1	3,9
41-50	3,0	7,0	6,4	5,8	7,1	4,4
51-60	3,3	7,0	6,8	5,8	7,5	3,9
61-70	—	7,0	6,6	6,4	5,8	3,6
71-80	—	6,3	5,0	5,9	4,3	3,0
81-85 (east boundary)	—	5,0	4,0	5,8	4,3	4,3
Mean	3,1	6,8	5,6	5,9	6,1	4,0

TABLE 3: The percentage frequency of occurrence (F_o) and percentage frequency of dense occurrence (F_i) of alien plants in the section of the Swakop River within the Namib Naukluft Park.

Distance from west (km)	<i>Argemone ochroleuca</i>		<i>Datura innoxia</i>		<i>Datura stramonium</i>		<i>Nicotiana glauca</i>		<i>Prosopis</i> spp.		<i>Ricinus communis</i>	
	F_o	F_i	F_o	F_i	F_o	F_i	F_o	F_i	F_o	F_i	F_o	F_i
0-10	—	—	100	100	100	20	100	—	100	60	80	—
11-20	—	—	100	100	100	30	100	20	100	60	30	—
21-30	10	—	100	100	90	20	100	30	100	70	40	—
31-40	—	—	100	100	100	20	100	80	100	50	90	—
41-50	10	—	100	100	100	50	100	30	100	30	90	—
51-60	10	—	100	100	100	80	100	20	100	90	70	—
61-70	—	—	100	100	100	60	100	50	80	20	50	—
71-80	—	—	100	70	50	—	90	20	70	—	40	—
81-85	—	—	100	17	100	—	100	50	33	—	50	—
Mean	3	—	100	92	93	33	99	35	90	52	66	—

TABLE 4: The abundance ratings (A) of alien plants in a 53 km section of the Kuseb River, downstream from Gobabeb.

Distance from west (km)	<i>Argemone ochroleuca</i>	<i>Datura innoxia</i>	<i>Datura stramonium</i>	<i>Nicotiana glauca</i>	<i>Ricinus communis</i>
0-10	5,3	6,3	5,4	6,7	3,0
11-20	4,8	6,5	4,5	6,8	4,0
21-30	6,6	6,3	5,2	7,0	-
31-40	5,3	7,6	7,0	7,0	5,0
41-50	5,0	6,5	6,7	6,9	3,0
51-54 (Gobabeb)	5,8	4,0	-	6,5	-
Mean	5,6	6,6	6,0	6,9	3,7

TABLE 5: The abundance ratings (A) of alien plants in a 75 km section of the Kuseb River, upstream from Gobabeb.

Distance from Gobabeb (km)	<i>Argemone ochroleuca</i>	<i>Datura innoxia</i>	<i>Datura stramonium</i>	<i>Nicotiana glauca</i>	<i>Ricinus communis</i>
0-01	5,7	6,7	3,8	6,0	3,0
11-20	6,6	6,0	3,8	6,6	4,0
21-30	6,5	7,0	4,0	4,6	6,9
31-40	3,5	7,0	-	3,0	6,1
41-50	6,4	7,0	3,0	5,8	6,7
51-60	6,5	7,0	3,3	6,3	6,2
61-70	6,9	7,0	4,7	6,7	5,4
71-75	7,0	7,0	4,8	6,8	6,0
Mean	6,3	6,9	4,2	6,1	5,9

TABLE 6: The percentage frequency of occurrence (F_o) and percentage frequency of dense occurrence (F_i) of alien plants in a 54 km section of the Kuseb River, downstream of Gobabeb.

Distance from west (km)	<i>Argemone ochroleuca</i>		<i>Datura innoxia</i>		<i>Datura stramonium</i>		<i>Nicotiana glauca</i>		<i>Ricinus communis</i>	
	F_o	F_i	F_o	F_i	F_o	F_i	F_o	F_i	F_o	F_i
0-10	40	20	90	70	70	20	100	90	20	-
11-20	60	10	80	70	40	10	100	80	10	-
21-30	100	80	90	60	50	10	100	100	-	-
31-40	40	10	100	100	100	100	100	100	10	-
41-50	50	20	80	50	60	50	100	90	20	-
51-54 (Gobabeb)	100	10	-	-	-	-	100	30	-	-
Mean	61	27	81	65	59	35	100	87	11	-

TABLE 7: The percentage frequency of occurrence (F_o) and percentage frequency of dense occurrence (F_i) of alien plants in a 75 km section of the Kuseb River, upstream from Gobabeb.

Distance from Gobabeb (km)	<i>Argemone ochroleuca</i>		<i>Datura innoxia</i>		<i>Datura stramonium</i>		<i>Nicotiana glauca</i>		<i>Ricinus communis</i>	
	F_o	F_i	F_o	F_i	F_o	F_i	F_o	F_i	F_o	F_i
0-10	70	40	60	50	40	-	80	40	20	-
11-20	90	80	70	50	40	-	100	70	60	-
21-30	60	50	100	90	30	-	80	-	100	90
31-40	40	-	100	100	-	-	10	-	80	50
41-50	70	40	100	100	10	-	90	40	100	80
51-60	100	50	100	100	30	-	100	60	100	40
61-70	90	80	100	100	90	-	90	70	100	30
71-75	100	100	100	100	100	-	100	80	100	60
Mean	76	52	91	85	39	-	68	43	81	43

ly in the upper region of the river, while *D. stramonium* was more frequently found in the lower region.

Prosopis spp. occurs in this river, downstream of the western boundary. However, no *Prosopis* spp. were found in the section of the Kuiseb within the park.

Tsondab and Tsauchab Rivers

D. innoxia was the most common alien plant species in these rivers, occurring with high abundance ratings in all regions (Tables 8 & 9). *A. ochroleuca* and *R.*

communis were found in both rivers but a much lower abundance ratings. *R. communis* occurred most frequently in the upper region of each river (Tables 10 & 11).

Four *Prosopis* spp. trees were found in the Tsauchab River, but this species was not detected in the Tsondab River. *N. glauca* occurred at fairly low abundance ratings throughout the Tsondab River, but was not detected in the Tsauchab River. A very small infestation of *D. stramonium* occurred in the middle region of the Tsondab River.

TABLE 8: The abundance ratings (A) of alien plants in the section of the Tsauchab River within the Namib Naukluft Park.

Distance from vlei (km)	<i>Argemone ochroleuca</i>	<i>Datura innoxia</i>	<i>Prosopis</i> spp.	<i>Ricinus communis</i>
0-1	—	8,0	3,0	—
2-11	—	4,7	—	—
12-21	—	6,7	—	—
22-31	—	7,0	3,0	3,0
32-41	—	6,7	—	3,0
42-51	—	7,0	3,0	6,8
52-61	3,0	7,0	—	4,4
62-70	4,3	6,7	3,0	3,0
Mean	4,0	6,3	3,0	5,1

TABLE 9: The abundance ratings (A) of alien plants in the section of the Tsondab River within the Namib Naukluft Park.

Distance from vlei (km)	<i>Argemone ochroleuca</i>	<i>Datura innoxia</i>	<i>Datura stramonium</i>	<i>Nicotiana glauca</i>	<i>Ricinus communis</i>
0-13	—	6,5	—	—	3,0
14-23	3,0	7,0	—	3,8	—
24-33	3,7	7,0	3,0	3,9	4,0
34-43	—	7,0	—	3,0	4,0
43-49	—	7,0	—	3,0	3,0
Mean	3,5	6,9	3,0	3,7	3,8

TABLE 10: The percentage frequency of occurrence (F_0) and percentage frequency of dense occurrence (F_i) of alien plants in the section of the Tsauchab River within the Namib Naukluft Park.

Distance from vlei (km)	<i>Argemone ochroleuca</i>		<i>Datura innoxia</i>		<i>Prosopis</i> spp.		<i>Ricinus communis</i>	
	F_0	F_i	F_0	F_i	F_0	F_i	F_0	F_i
0-1	—	—	100	100	100	—	—	—
2-11	—	—	90	20	—	—	—	—
12-21	—	—	100	80	—	—	—	—
22-31	—	—	100	100	10	—	10	—
32-41	—	—	100	90	—	—	20	—
42-51	—	—	100	100	10	—	80	—
52-61	10	—	100	100	—	—	50	—
62-70	50	—	100	78	11	—	20	—
Mean	8	—	99	84	4	—	27	—

TABLE 11: The percentage frequency of occurrence (F_0) and percentage frequency of dense occurrence (F_i) of alien plants in the section of the Tsondab River within the Namib Naukluft Park.

Distance from vlei (km)	<i>Argemone ochroleuca</i>		<i>Datura innoxia</i>		<i>Prosopis</i> spp.		<i>Nicotiana glauca</i>		<i>Ricinus communis</i>	
	F_0	F_i	F_0	F_i	F_0	F_i	F_0	F_i	F_0	F_i
0-13	—	—	85	54	—	—	—	—	8	—
14-23	10	—	100	100	—	—	80	—	—	—
24-33	30	—	100	100	10	—	90	—	10	—
34-43	—	—	100	100	—	—	10	—	60	—
44-49	—	—	83	83	—	—	17	—	17	—
Mean	8	—	95	89	2	—	39	—	20	—

Awasib and Koichab Rivers

No alien invasive plants were found in these rivers. One of the tributaries of the Koichab River on the farm Alabama (No. 140) was noted to contain several plants of *D. innoxia* just outside of the park boundary.

DISCUSSION

The limitations of this type of census must be recognized and the results are presented with this in mind. No attempt has been made to determine precise density counts of alien plants. One transect along the centre of each river yielded data on the visible plants. Variable river widths, multiple channels, different sampling times and conditions and a multitude of other factors rule out precise counts.

It is also possible that small, less obvious species may have been overlooked. For example one *Prosopis* spp. tree and a few *D. ferox* L. (Large Thorn Apple) plants have been recorded in the Kuiseb River subsequent to this census.

The data presented do, however, give an indication of the status of alien plants in this region and can be used by managers in making decisions regarding the control of alien species.

In addition this type of survey has the advantage of repeatability. Each river took a day or less to survey and further surveys will be possible even in the absence of experienced observers.

Ecological aspects

Of the rivers surveyed, the Swakop and Kuiseb Rivers had the highest abundance ratings of alien plants.

In the upper 25 km of the Swakop River *Prosopis* spp. was almost absent, the result of manual removal of this species between 1985 and 1988. The reduced occurrence of other alien species in this region may also be due to human activity and removal, despite being non-target species.

In the Kuiseb River two species, *D. innoxia* and *R. communis*, occurred less frequently and at lower abundance rates in several sections than in other areas. In most of these sections Topnaar goats are kraaled and watered and the reduced abundance, and often absence of these two species in areas close to the goat kraals suggests a correlation. *R. communis* is heavily browsed by goats and *D. innoxia* seedlings appear to suffer from the trampling effect of the goat-herds (Vinjevoeld *et al.* 1985).

In the upper portions of the Kuiseb River and in the other rivers surveyed where goats are absent, indigenous large herbivores are more common, but browsing and trampling of alien plants has not been observed. Baboons *Papio ursinus* utilize *N. glauca* (C. Brain pers. comm.), but this impact is very localized and probably has little effect on the viability of this species.

In the upper region of the Kuiseb River *D. innoxia*, *A. ochroleuca* and *R. communis* occurred with high abundance and frequency of occurrence ratings. This section of the river receives flood waters more frequently than the lower regions and the higher density of these alien plants may be related to this. Similarly the increased frequency and abundance of *R. communis* and *A. ochroleuca* in the upper regions of the Tsondab and Tsauchab Rivers may be due to the more frequent availability of surface water.

D. innoxia was the most common alien species in the Tsondab and Tsauchab Rivers, having similar abundance and frequency of occurrence ratings as in the Kuiseb River. Other species were less common in the Tsondab and Tsauchab Rivers than the Kuiseb River, with the exception of *Prosopis* spp. which was not found in the Kuiseb River.

While the Awasib and Koichab Rivers appear to be free of alien plants at present, the occurrence of *D. innoxia* on the park boundary in the Koichab River catchment area and of many *Prosopis* spp. trees on the farms within the catchment areas of both of these rivers, suggests that under suitable conditions infestations could occur.

The results of a similar census of the Swakop River and a portion of the Kuiseb River performed in 1984 (Macdonald & Nott 1987) can be compared to the present census.

In the Swakop River *Prosopis* spp. occurred at the same frequency in both censuses, but appeared to be more abundant in the present survey.

A. ochroleuca occurred at the same rating, whereas *D. innoxia*, *D. stramonium* and *R. communis* were not recorded in 1984. *N. glauca* has increased in both frequency and abundance.

Prior to the 1984 census (Macdonald & Nott 1987) several small flows of surface water were recorded in the Swakop River, upstream of the eastern park boundary (Unpubl. data, Division Hydrology, Dept. of Water Affairs, S.W.A./Namibia). Whether these floods reached the park is unknown, but if so, they were likely to have had little effect on the river vegetation. Apart from these small floods no other floods were recorded in the Swakop River between 1977 and 1984. Since 1984 several large floods have passed through the park, in 1985 and in 1988, while a small flood was recorded east of the park in 1986 (Unpubl. data, Division Hydrology, Dept. of Water Affairs, S.W.A./Namibia).

It is therefore suggested that a large amount of the variation between the 1984 and the present surveys can be attributed to the different amounts of flood waters received prior to each survey, reflecting the dependence of these alien species on water.

The sections of the Kuiseb River censused by Macdonald and Nott (1987) correspond to the first 20 km of the region upstream of Gobabeb. All species record-

ed in the present census were found in the 1984 census. *A. ochroleuca* and *D. innoxia* occurred more frequently and in greater abundance, while *D. stramonium* was less common in the present survey than in 1984.

The Kuiseb River flowed for the first time in six years in 1984 (M. Seely pers. comm.), and has flowed every year since (D.C.B. pers. obs.). As both censuses occurred following a flood the similarity of the results is not unexpected.

Management recommendations

One of the main aims of natural parks is to "maintain biotic diversity" and therefore the introduction and continued existence of any alien flora or fauna should be prevented if at all possible. While alien plants, particularly if they are invasive species, are considered undesirable in any conserved area, some species may be so abundant and occur with such frequency that their removal cannot be economically justified. In such instances indigenous species from the previously natural plant community may be lost.

Most of the alien plant species occurring in this region have originated from river catchment areas on the escarpment (Brown & Gubb 1986). These areas are outside of the park and constitute a seed source over which the authorities have little control. As alien plants are unlikely to be eradicated from these areas, reinfestation of conserved areas will be a continual problem. Unless biological control is introduced, manual control of alien plants must be an annual activity in order to be effective.

At present, the manual removal of alien plants and chemical poisoning of individual plants are the only feasible control methods accepted within the Namib Naukluft Park. As these are time-consuming and expensive, research into other methods of control, such as biological control, should be encouraged. *Ad hoc* observations suggest that *Prosopis* spp. can out-compete indigenous vegetation (Vinjevoold *et al.* 1985). This has resulted in considerable effort being expended to eradicate this species from the Swakop River. Little is known of the competitive abilities of the other alien plant species occurring in the Namib, and ecological studies on these plants are required.

Some alien species may now form part of a climax vegetation community, as *Prosopis* spp. appears to do in parts of the Swakop River. If a species is found to be actively invading a community, its removal must be of higher priority than the removal of those species which already form part of a climax community. Studies to determine which species should be given highest management priority are urgently required.

In general the perennial alien species *N. glauca*, *R. communis* and *Prosopis* spp. occurred at lower abundances and had lower frequencies of occurrence than the annual species. Perennial species are slower growing and the mere fact of their greater longevity and potential impact on the local vegetation makes them

more important and easier to control than annuals. They occur mainly on the banks of the main river channels, usually in association with the indigenous vegetation. The potential for competitive impact is therefore present and *ad hoc* observations indicate that in some areas the local vegetation has suffered from the presence of these alien species (D.C.B. pers. obs.).

R. communis occurred in all four of the northern rivers, but dense infestations were found only in the Kuiseb River. *R. communis* now occurs throughout the Kuiseb River and may be actively invading sections where it was absent several years ago (D.C.B. pers. obs.). This could also be a result of changes in the environment enabling a succession of plant communities to occur. Between 1979 and 1983 the Kuiseb received little flood water (M. Seely pers. comm.). *R. communis* seems to require fairly moist conditions and from 1984 until the present, the Kuiseb has flowed regularly (pers. obs.) providing an ideal environment for vigorous growth and expansion of this species.

The status of *R. communis* is under question, with some authorities maintaining that it is indigenous to the area (Lenssen in prep.) Archaeological evidence suggests that this species occurred in the Namib over 3000 years B.P. (Sandelowsky 1977). Deacon (1986) suggested that it was introduced by stoneage man and therefore should still be considered alien. Until its status has been determined, any populations which are shown to be invading an area should be controlled.

The central river bed region of desert ephemeral rivers is being occupied by annual or relatively short-lived perennial alien species; *D. innoxia*, *D. stramonium* and *A. ochroleuca*. As this area normally contains few indigenous plants (D.C.B. pers. obs.) these alien species are thought to have little direct impact on indigenous vegetation.

D. innoxia is beyond mechanical control in all of the northern river systems. Dense infestations occurred in more than 80% of all river sections. Biological control of this species is the only realistic control method that is acceptable in conservation areas. A potentially new infestation of *D. innoxia* may be imminent in the Koichab system. Encouragement and assistance should be given to boundary farmers in this region to eradicate this species before it enters the park.

Macdonald and Nott (1987) suggested that as *D. stramonium* may be competitively inferior to its congener *D. innoxia* eradication is unnecessary. The present survey yielded no evidence that *D. stramonium* occurred in greater densities in areas of reduced *D. innoxia* abundance as would be expected, although abiotic conditions may have masked such processes. As *D. stramonium* was absent from the Tsauchab River and only one plant was found in the Tsondab River, it should be easily controlled in these rivers. *D. stramonium* had a fairly high frequency of occurrence in the Kuiseb and Swakop Rivers, but dense infestations oc-

curred only in the latter. However, until it is shown to have some impact on the indigenous vegetation removal of this species should not be given priority.

As dense infestations of *A. ochroleuca* occurred in over 50% of the sections of the Kuiseb River it would be difficult to eradicate. In the other rivers this species occurred with very low abundance ratings or was absent. It may be possible to control in these rivers, but until it has been shown to have an impact on the indigenous vegetation, removal should be considered to be of a low priority.

SUMMARY

The populations of alien plants in rivers of the Namib Naukluft Park were investigated and the rivers were assessed for degree of infestation. Management recommendations based on these results suggest that highest priority should be given to the removal of the perennial species; *Prosopis* spp., *N. glauca* and *R. communis* (Table 12). These species should be removed immediately from the Tsondab and Tsauchab Rivers and reinfestations searched for and removed annually.

If maintenance of natural species diversity is to be accorded high priority for the Namib Naukluft Park, these three species should be removed from the Swakop and Kuiseb Rivers.

Research into the competitive ability and impact of alien plant species on the indigenous vegetation should be initiated.

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TABLE 12: A summary of management recommendations to eradicate alien invasive plants from the rivers of the Namib Naukluft Park.

Species	Annual/ Perennial	Probable ecological effect	Present method of eradication	Priority rating
<i>Prosopis</i> spp.	Perennial	High	Mechanical/chemical	High
<i>R. communis</i>	Perennial	Medium	Mechanical	Medium
<i>N. glauca</i>	Perennial	Medium	Mechanical	Medium
<i>D. innoxia</i>	Annual	Locally high	None	Locally high
<i>D. stramonium</i>	Annual	Little	None	Low
<i>A. ochroleuca</i>	Annual	Little	None	Low

Birds and electricity transmission lines in South West Africa/Namibia

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ABSTRACT

1447 km of 330 kV and 220 kV electricity transmission lines in South West Africa/Namibia were surveyed from a helicopter. Only one collision victim, a secretarybird *Sagittarius serpentarius*, was found, and there was no evidence of bird electrocution. Six raptor species and three passerines were found breeding on transmission towers. Blackbreasted snake eagles *Circaetus gallicus*, pale chanting goshawks *Melierax canorus* and greater kestrels *Falco rupicoloides* were the most common raptors, but the overall raptor inter-nesting distance (mean of 76 km) was large. The only power distributions due to birds were on 220 kV lines where these passed close to large water impoundments; "flashovers" occurred when fish-eating species excreted onto insulators.

INTRODUCTION

A network of over 5 000 km of electricity transmission lines of 66 kV to 330 kV carries power from the generating stations to the most important points of consumption in South West Africa/Namibia (van der Merwe 1983). The powerlines and their supporting towers (pylons) cross most of the vegetation types of the country, extending from the Namib coast in the west to the Kalahari in the east, and from the Cunene River in the north to the Orange River in the south (Figure 1). Because the best potential for power generation is in the extreme north of the country (hydroelectricity), far from the points of highest consumption, large overhead cables will be a part of our landscape for many years to come.

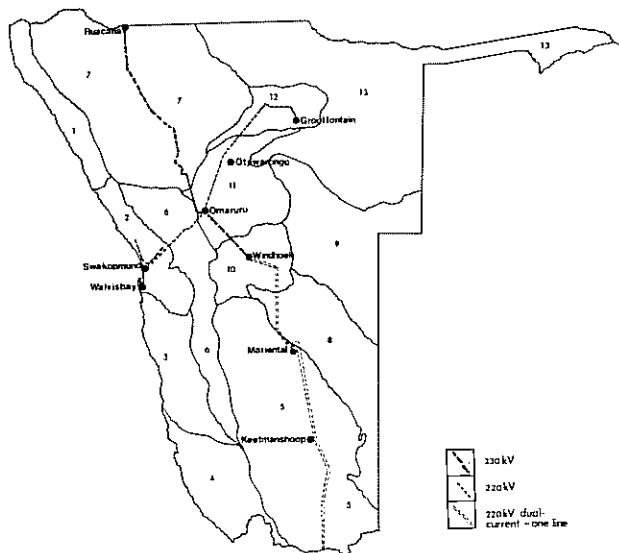


FIGURE 1: Localities of the 330 kV and 220 kV transmission lines in SWA/Namibia showing those sections surveyed, and the vegetation types (after Giess 1971) through which they pass. Regions 1, 2 & 3 = Northern, Central and Southern Namib (<100 mm of rainfall per annum), 4 = Southern winter rainfall Namib (<100 mm), 5 = Dwarf Shrub Savanna (100-200 mm), 6 = Desert-Savanna Transition (100-200 mm), 7 = Mopane Savanna (300-400 mm), 8 = Southern Kalahari Savanna (200-300 mm), 9 = Camelthorn Savanna (300-400 mm), 10 = Highland Savanna (300-400 mm), 11 = Thornbush Savanna (400-500 mm), 12 = Mountain Savanna (500-600 mm), 13 = Woodlands (400-600 mm).

Electricity brings obvious advantages to a developing country, but there are a number of ecological interactions associated with electricity transmission in overhead cables that have been identified in other countries and which should not be overlooked. These interactions can be divided into three main groups.

Negative ecological factors

a) Birds collide with overhead cables. This has been reported frequently for waterfowl in areas where powerlines pass near wetlands, e.g. Heijnis 1980; Longridge 1986; Rusz *et al.* 1986, but has also been reported elsewhere, involving a number of rare and endangered species, e.g. white stork *Ciconia ciconia* (Cramp & Simons 1977; Fiedler & Wissner 1980; Oatley & Rammesmayr 1988), greater *Phoenicopterus ruber* and lesser *P. minor* flamingoes (Brooke 1984; Hobbs & Ledger 1986), wattled crane *Grus carunculata* (Johnson & Sinclair 1984), European griffon *Gyps fulvus* (Terrasse 1983) and California condor *Gymnogyps californianus* (Snyder 1983).

b) Some bird species are electrocuted on towers while landing and taking off. The best document case in southern Africa involves the endemic Cape vulture *Gyps coprotheres* (e.g. Markus 1972; Ledger 1980, 1984; Ledger & Annegarn 1981; Hobbs & Ledger 1986). On a section of about 140 km of transmission lines in the Transvaal Province, 165 vultures were electrocuted in three years. Many other large species have been similarly affected, e.g. European griffon (Terrasse 1983; Mendelssohn & Leshem 1983; Leshem 1983 - a quarter of Israel's northern population was electrocuted in two years), Egyptian vulture *Neophron percnopterus* (Nikolaus 1984), lappetfaced vultures *Torgos tracheliotus*, white and black *Ciconia nigra* storks and golden eagles *Aquila chrysaetos* (Fiedler & Wissner 1980; Haas 1980; Leshem 1985), martial eagles *Polemaetus bellicosus* (Brooke 1984) and black eagles *A. verreauxii* (Boshoff & Fabricius 1986).

c) Powerlines are unsightly, and particularly in nature reserves, they are aesthetically unacceptable.

Positive ecological factors

a) Some birds nest on the towers of transmission lines. These towers provide birds with secure, high nest sites and in some cases have allowed species to expand their breeding range into areas where no natural nesting sites occur (Newton 1979), e.g. martial and black eagles in the Karoo (Boshoff 1986; Boshoff & Fabricius 1986; Ledger *et al.* 1987). Table 1 lists the species that have been recorded nesting on electricity towers in southern Africa.

TABLE 1: Bird species that have been reported to nest on electricity transmission towers in southern Africa.

Species	Source
Hateda Ibis <i>Bostrychia hagedash</i>	Ledger & Hobbs 1985
Egyptian Goose <i>Alopochen aegyptiacus</i>	Ledger & Hobbs 1985
Whitebacked Vulture <i>Gyps africanus</i>	Ledger & Hobbs 1985
Black Eagle <i>Aquila verreauxii</i>	Boshoff & Fabricius 1986 Ledger <i>et al.</i> 1987
Tawny Eagle <i>Aquila rapax</i>	Dean 1975; Tarboton & Allan 1984
African Hawk Eagle <i>Hieraaetus fasciatus</i>	Tarboton & Allan 1984
Martial Eagle <i>Polemaetus bellicosus</i>	Dean 1975; Boshoff <i>et al.</i> 1983; Tarboton & Allan 1984
Lanner Falcon <i>Falco biarmicus</i>	Kemp 1972; Tarboton & Allan 1984
Rock Kestrel <i>Falco tinnunculus</i>	Boshoff <i>et al.</i> 1983
Greater Kestrel <i>Falco rupicoloides</i>	Kemp 1978, 1984
Black Crow <i>Corvus capensis</i>	Kemp 1984; Ledger & Hobbs 1985
Pied Crow <i>Corvus albus</i>	Kemp 1984; Ledger & Hobbs 1985

b) Many birds roost (overnight) and perch on transmission lines and towers (e.g. Ledger 1980, 1988; Ledger & Annegarn 1981; Steyn 1982; Kemp 1984). These structures provide the birds with a secure perch as well as an elevated position from which to hunt for prey.

Negative economic factors

a) Roosting birds may excrete onto insulators supporting transmission cables and thereby reduce their insulating properties and cause "flashovers", thus disrupting supply. This has been found mainly with ibises, herons and egrets near wetland areas (Ledger 1980, 1988; Hobbs & Ledger 1986).

b) Electrocutation of birds can cause disruptions in electricity supply ranging from momentary interruptions due to impedance faults from phase to earth, or over-current faults due to overloading of a phase, to long interruptions of many hours because of damage to conductors (Ledger 1984, 1988).

c) Large nest structures, particularly when wet after rainfall, can similarly cause flashovers and may ignite, disrupting the power supply and possibly damaging equipment.

It was therefore decided to investigate electricity transmission lines and towers in SWA/Namibia to determine (a) to what extent, if any, these structures were leading to electrocution and collision in birds, (b) what species were in turn using the structures for nesting and perching and (c) what disruptions these activities were having on the electricity supply of the country.

METHODS

Opportunistic use was made of transit flights by helicopters under contract of the SWA/Namibia Directorate of Nature Conservation (a Bell 47 and a Bell Jet Ranger) to survey the large 330 kV and 220 kV electricity transmission lines where these lines coincided with routes to and from scheduled destinations. The crew consisted of a pilot and one observer. Normal survey height was about 20 m above the top of the steel towers and about 30 m to one side, flying parallel to the lines on the downwind side. For closer inspections of particular sites and to photograph nests, slow passes were made, or the aircraft was held stationary in the appropriate position.

A total of 1 447 km of transmission lines were surveyed on four routes, including 3106 support towers (Figure 1; Table 2). The following data were recorded:

- habitat type (after Giess 1971),
- design of support tower and voltage rating (see Figure 2),
- the presence or absence of electrocution victims at the base of each tower,
- collision victims in the strip below the transmission lines,
- nests in the transmission towers. The bird species involved was recorded as well as the position of the nest in the tower,
- all species perching on the towers or cables of about rock kestrel *Falco tinnunculus* size or larger, together with their position.

Reports of the South West Africa Water and Electricity Corporation (SWAWEC) referring to causes of power disruptions each month were analysed covering the two-year period 1986 and 1987.

RESULTS

Electrocution and collision

Three different steel tower structures (Figure 2) were examined during this survey, covering 687 towers of design A, 1 413 of design B and 1 006 of design C. No electrocution victims were found.

The survey covered 1 447 km of transmission lines, about 70% of the total length of all 330 kV and 220 kV lines in this country, in seven different vegetation

TABLE 2: Transmission lines surveyed from a helicopter (see Figure 1) with dates, times, distances, tower design (Figure 2) and numbers of towers.

Route (aircraft)	Date	Time	Distance (km)	Speed (km/h)	Tower design	Number of towers
1. Rossing (42 km ENE of Swakopmund) to Gerus (26 km NW of Otjiwarongo) (Bell 47)	15/08/86	13h50 to 16h40	335	150	A 220 kV	687
2. Grunau to Hardap Dam (Bell 47)	19/10/86	10h45 to 15h00	412	130	B 220 kV	833
3. Hardap Dam to Windhoek (Bell 47)	21/10/86	07h10 to 11h45	278	152	B 220 kV	580
4. W boundary of Etosha (18°52'S/14°38'E) to Okahandja (Bell Jet Ranger)	22/04/87	11h45 to 14h50	422	153	C 330 kV	1006
TOTALS	4 days	10 h*	1 447	145		3 106

* Number of flying hours along transmission lines excluding ferry time to the lines and refueling times.

TABLE 3: Bird species recorded nesting on electricity transmission towers during aerial surveys and the numbers of nests, in seven vegetation types in SWA/Namibia (see Figure 1).

Transmission lines surveyed: Distance (km)	Vegetation types							Totals
	2	5	6	7	8	10	11	
: No. towers	103	1 080	198	554	121	212	838	3 106
Species								
Brown Snake Eagle <i>Circaetus cinereus</i>	-	-	-	-	-	-	1	1
Blackbreasted Snake Eagle <i>Circaetus gallicus</i>	-	3	-	2	-	-	-	5
Pale Chanting Goshawk <i>Melierax canorus</i>	-	3	-	-	-	-	-	3
Lanner Falcon <i>Falco biarmicus</i>	-	2	-	-	-	-	-	2
Rock Kestrel <i>Falco tinnunculus</i>	-	2	-	-	-	-	-	2
Greater Kestrel <i>Falco rupicoloides</i>	-	3	-	-	-	-	-	3
Unidentified raptor nest	1	1	1	-	-	1	-	4
Totals for raptors	1	14	1	2	0	1	1	20
Totals per 100 km	2,0	4,6	1,0	0,8	0	1,1	0,3	1,4
Black Crow <i>Corvus capensis</i>	-	6	3	2	-	-	-	11
Redbilled Buffalo Weaver <i>Bubalornis niger</i>	-	26	39	280	4	308	871	1 528
No. RBBW nests/10 towers	0	0,2	2,0	5,1	0,3	14,5	10,4	4,9
Social Weavers <i>Philetairus socius</i>	-	13	2	-	117	-	-	132
No. SW nests/10 towers	0	0,1	0,1	0	9,7	0	0	0,4

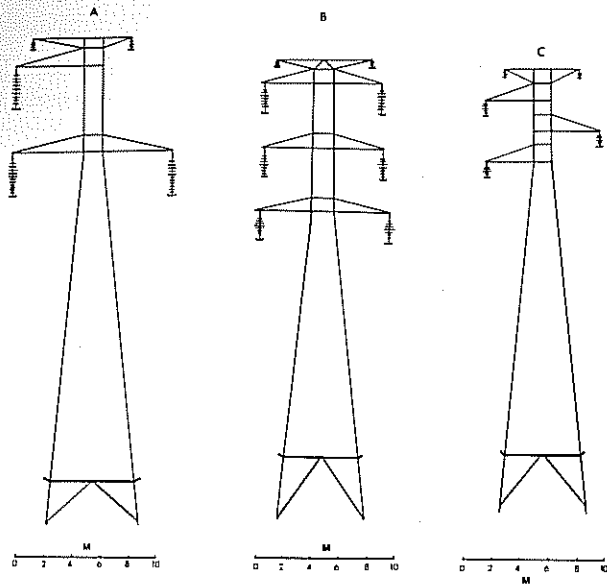


FIGURE 2: Electricity transmission towers surveyed in SWA/Namibia. A = 330 kV tower, B = 220 kV dual current tower and C = 220 kV tower.

types. Only one collision incident was recorded, a secretarybird *Sagittarius serpentarius* found freshly dead below the powerlines near Gibeon in Dwarf Shrub Savanna habitat.

Nests

Six species of raptors and three of passerines were found nesting on the 330 kV and 220 kV electricity towers (Table 3). Raptors bred at low densities on the towers with an overall linear inter-nest distance of 76 km. Nesting density was inversely related to rainfall (Figure 3) and was highest in the Dwarf Shrub Savan-

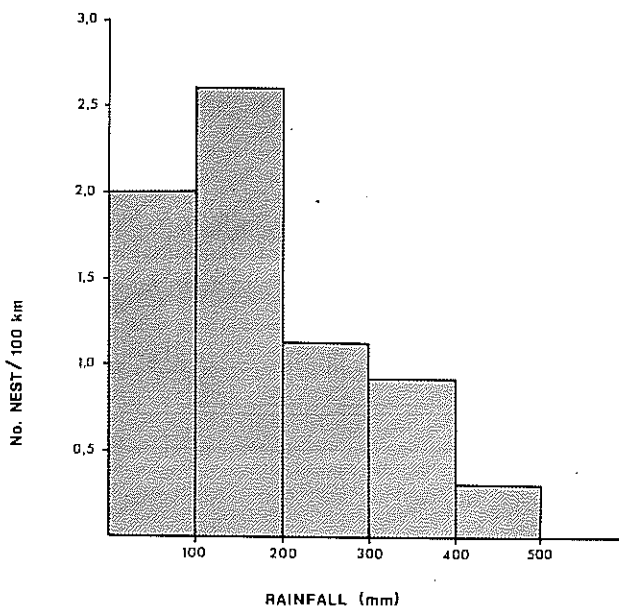


FIGURE 3: Number of raptor and crow nests per 100 km of transmission lines surveyed, plotted against rainfall.

na in the south of the country. The blackbreasted snake eagle *Circaetus gallicus* was the most common raptor species nesting on electricity towers (n = 5) followed by pale chanting goshawks *Melierax canorus* and greater kestrels *Falco rupicoloides* (n = 3 each).

There were few black crow *Corvus capensis* nests in towers, which was probably the reason for the low number of *Falco* species. Redbilled buffalo weavers *Bubalornis niger* were the most common birds found nesting in the towers. They were at highest densities in the Highland, Thornbush and Mopane Savanna regions and were uncommon in areas of less than 300 mm of rain per annum, except along large river courses. Sociable weaver *Philetairus socius* nests on towers were confined mainly to the southern Kalahari Savanna.

Black crows and pale chanting goshawks built nests only at low levels on the towers (position 6, Figure 4) and thus all but one nest occupied by *Falco* species were in this position (Table 4). The exception was a pair of lanner falcons *Falco biarmicus* occupying the nest of a large, unknown raptor at the top of the tower. The snake eagles nested in the main structure of the towers (as opposed to the side-arms supporting the conductors), mainly in the top struts (position 1) but also in the cross struts one level lower (position 3).

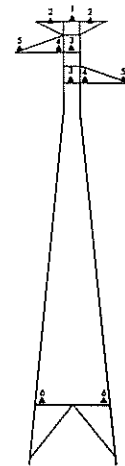


FIGURE 4: A general transmission support tower showing positions of nests and perched birds (see Tables 4 & 6).

All sociable weaver nests were built low on the corners of the towers around the anti-climbing wires (position 6) and 80% of redbilled buffalo weaver nests were in this position. Once the four corners of a tower had been occupied the buffalo weavers then occupied sites higher up the tower, either within the main structure (position 3) or at the junction of the side-arms and the main structure (position 4). Occupancy of sites at the ends of the side-arms and thus above the insulator and conductor (position 5) constituted only 2% of sites used by these birds and were used only once other sites were occupied. In addition, only in specific geographic localities were nesting densities so high as to result in buffalo weavers building nests in this position. These

TABLE 4: Position of nests on 330 kV and 220 kV electricity transmission support towers (see Figure 4) in SWA/Namibia.

Species	No. of nests in positions 1-6						Total
	1	2	3	4	5	6	
Brown Snake Eagles <i>Circaetus cinereus</i>	-	-	1	-	-	-	1
Blackbreasted Snake Eagle <i>Circaetus gallicus</i>	4	-	1	-	-	-	5
Pale Chanting Goshawk <i>Melierax canorus</i>	-	-	-	-	-	3	3
Lanner Falcon <i>Falco biarmicus</i>	-	1	-	-	-	1	2
Rock Kestrel <i>Falco tinnunculus</i>	-	-	-	-	-	2	2
Greater Kestrel <i>Falco rupicoloides</i>	-	-	-	-	-	3	3
Unidentified raptor nests	1	1	2	-	-	-	4
Black Crow <i>Corvus capensis</i>	-	-	-	-	-	11	11
Totals	5	2	4	0	0	20	31
Redbilled Buffalo Weaver <i>Bubalornis niger</i>	-	-	126	167	31	1 204	1 528
% Rb. B. W.	0	0	8	11	2	79	100
Sociable Weaver <i>Philetairus socius</i>	-	-	-	-	-	132	132

localities were where powerlines (i) ran near to or crossed large river courses and (ii) ran near the bases of large hills or mountain ranges, i.e. both sites more mesic than those surrounding.

Perching birds

Twelve species of birds, of rock kestrel size and larger, were found perching on the transmission towers (Table 5). Pale chanting goshawks were most common (48% of all birds recorded) followed by blackbreasted snake eagles (22%) and rock kestrels (13%). Most birds (95%) were perched on or in the top third of the towers while the remainder were at position 6 (see Figure 4). The top lattices (positions 1 & 2) were selected as perch sites by 60% of the birds and the outer arms (positions 5) by 7%, while 28% of birds perched within the top third of the structure (positions 3 & 4) (Table 6). The use of these different perch sites depended on the species involved. Martial eagles, the snake eagles and pale chanting goshawks preferred the top struts of the towers whereas African hawk eagles and rock kestrels preferred perching within the structure.

Power failures

For the 330 kV lines lightning (44%) and veld fires (29%) were the main causes of disruption (Figure 5), and they were both highly seasonal (Figure 6). No disruptions were caused by birds. On the 220 kV lines lightning was the main cause of disruption (64%) followed by bird pollution on insulators (17%). Bird pollution was restricted to powerlines at two localities, the

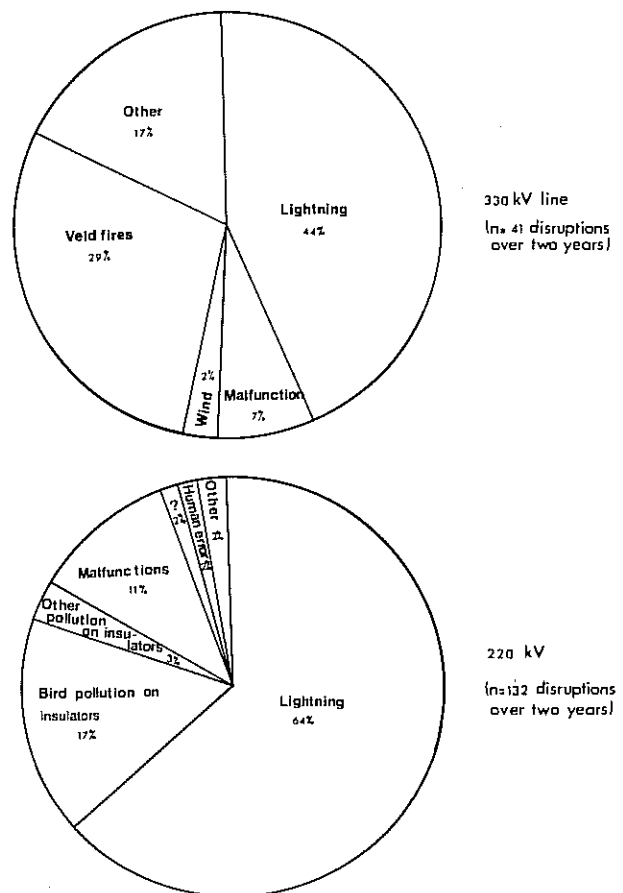


FIGURE 5: Causes of power disruption on the 330 kV and 220 kV line in SWA/Namibia during 1986 and 1987.

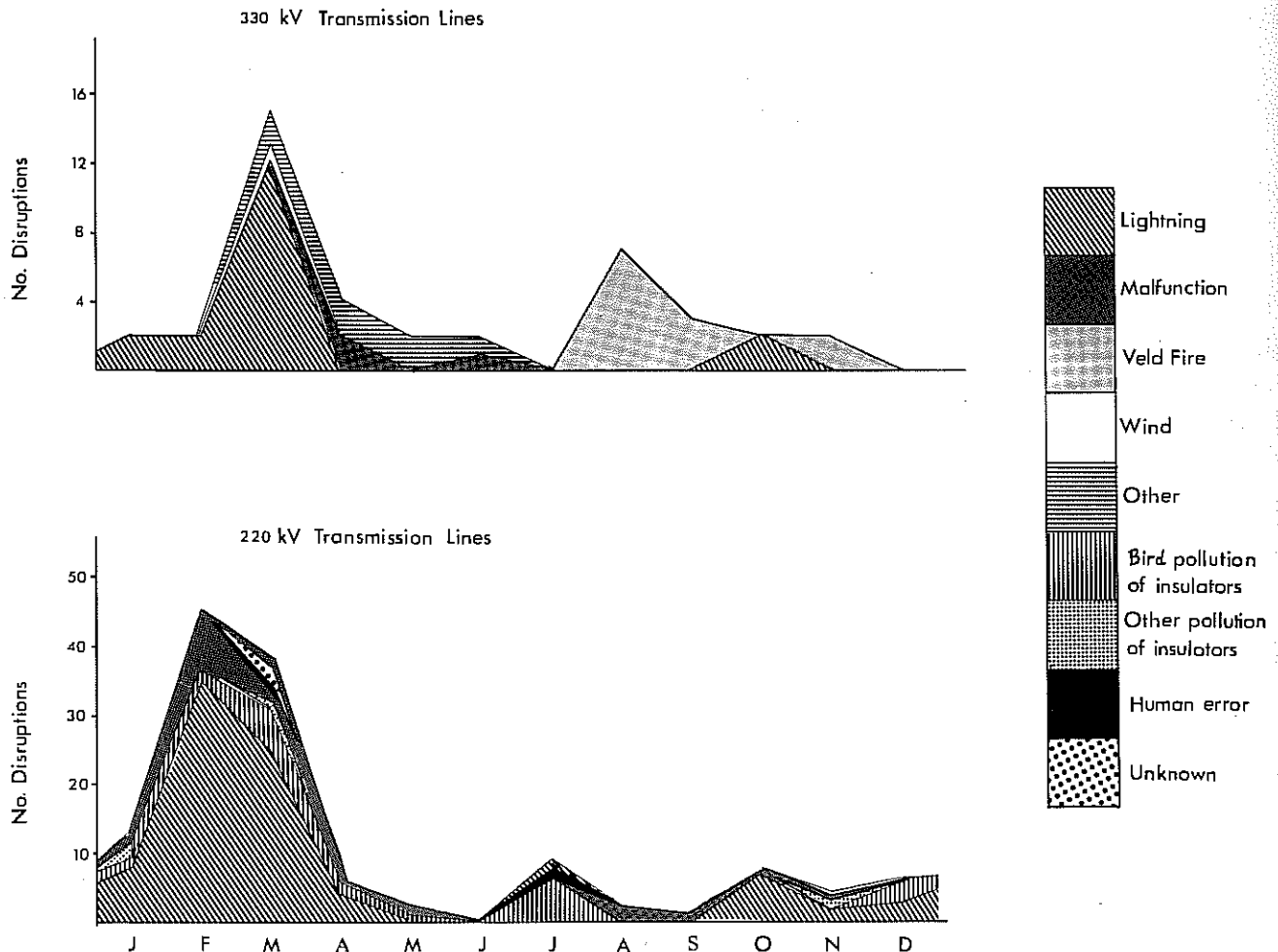


FIGURE 6: Seasonal incidents of power disruptions on the 330 kV and 220 kV lines in SWA/Namibia during 1986 and 1987.

Hardap Dam and the Goreangab Dam. The pollution was caused by the excreta of fish-eating birds. A subsequent check at Goreangab Dam found grey herons *Ardea cinerea* and reed cormorants *Phalacrocorax africanus* roosting on the pylons and local inhabitants reported that white pelicans *Pelecanus onocrotalus* and whitebreasted cormorants *Phalacrocorax carbo* also sometimes roosted there. No other power failures due to birds were reported. Other animals, a snake and a baboon, caused two power disruptions.

DISCUSSION AND RECOMMENDATIONS

Heijnis (1980) found that, in Holland, 70% of carcasses under transmission lines were scavenged within 24 h. This would indicate that counts such as those carried out in this survey in SWA/Namibia would provide absolute minimum figures. In the south of this country (region 5, where 40% of the survey was conducted), the numbers of scavenging animals have been drastically reduced by farmers using poisoned baits for mammalian predators (Brown 1986). Avian scavengers have been reduced to just 16% of their potential numbers based on a conservative estimate of available carrion (Brown 1988). While some carcasses

might have been scavenged from under the transmission lines, this is unlikely to be as prevalent as in Heijnis' study. The incidence of electrocution and collision involving the 330 kV and 220 kV lines surveyed is therefore considered to be generally low. However, it should be borne in mind that not all collision victims die on impact, but may break wings and move away from the power lines. Also, the incidents of bird collision with powerlines may be seasonal (Longridge 1986), e.g. young flamingoes moving between their inland natal areas and the coast.

The nesting density of raptors on transmission towers was inversely proportional to rainfall, presumably because in low rainfall areas large trees available for birds to nest in are limited in number. However, the generally low density of raptors nesting on towers was surprising, particularly in the Dwarf Shrub Savanna region. In similar Karoo vegetation in the Cape Province, Boshoff (1986) found 12–13 pairs of martial eagles (18 nests) at a mean inter-pair distance of 23 km. This is a smaller inter-pair distance than for all raptor species combined in the Dwarf Shrub Savanna region of SWA/Namibia (38 km between nesting pairs), where no nesting martial eagles were found.

TABLE 5: Bird species of Rock Kestrel size and larger recorded perching on transmission towers during aerial surveys in seven vegetation types in SWA/Namibia (see Figure 1).

Transmission lines surveyed: Distance (km)	Vegetation types							Totals
	2	5	6	7	8	10	11	
: No. towers	103	1 080	198	554	121	212	838	3 106
Species								
Tawny Eagle <i>Aquila rapax</i>	—	—	—	—	1	1	—	2
African Hawk Eagle <i>Hieraaetus fasciatus</i>	—	1	—	2	—	—	5	8
Martial Eagle <i>Polemaetus bellicosus</i>	—	2	—	1	2	1	—	6
Brown Snake Eagle <i>Circaetus cinereus</i>	—	—	—	1	—	1	4	6
Blackbreasted Snake Eagle <i>Circaetus gallicus</i>	2	21	2	17	1	4	14	61
Augur Buzzard <i>Buteo augur</i>	—	—	—	—	—	1	—	1
Blackshouldered Kite <i>Elanus caeruleus</i>	—	2	—	—	—	—	—	2
Pale Chanting Goshawk <i>Melierax canorus</i>	—	57	4	35	2	2	32	132
Lanner Falcon <i>Falco biarmicus</i>	—	9	—	—	1	—	—	10
Rednecked Falcon <i>Falco chicquera</i>	—	1	—	—	—	—	—	1
Rock Kestrel <i>Falco tinnunculus</i>	—	9	6	6	—	2	12	35
Greater Kestrel <i>Falco rupicoloides</i>	—	10	2	—	—	—	—	12
Totals	2	112	14	62	7	12	67	276
Total / 100 km	4,0	21,0	14,4	26,3	11,3	12,8	17,9	19,1

The habit of nesting on transmission towers may be a function of time; a bird raised in a tower nest may be more likely to choose such a site itself. However, the low number of nests found on these surveys would suggest that nests were being removed by the SWAWEC maintenance linemen. In the past, bird nests were known to cause "flashovers", particularly during rainy weather (P. Hoogenhout pers. comm. 1988). The species responsible was mainly the red-billed buffalo weaver. The nests of these birds, when situated near conductors, are therefore removed by the linemen. It is doubtful whether they are able to distinguish between the nests of these species and those of raptors and crows. The geographic localities where redbilled buffalo weavers build in the upper levels of towers (because the lower levels are already occupied by nests of conspecifics) are fairly specific; where powerlines pass near to large river courses and at the bases of hills. These localities could be mapped by the linemen and they could confine their nest-removing

activities to these places. This would save on costs for SWAWEC and leave the other bird species, which cause few or no problems, undisturbed.

During 1986 and 1987 the only cause of power disruption due to birds was pollution by their excreta on conductors on towers near large water bodies. Since then, perch guards have been fitted above the conductors to prevent birds perching and roosting in these positions (P. Hoogenhout pers. comm. 1988). The effectiveness of this measure is still being evaluated.

Because the continual removal of raptor and crow nests from transmission towers is costly, time consuming, destructive to the birds and unnecessary, the following recommendations are offered, based largely on the findings of Olendorff *et al.* (1981) & Ledger (1983, 1988).

1. If nests are removed, the birds will usually rebuild. The chances of sticks being dropped and causing "flashovers" will thus be increased. Whenever possi-

TABLE 6: Site selection by birds perching on electricity transmission towers in SWA/Namibia. "Top" = positions 1 & 2, "side arms" = positions 5, "within" = positions 3 & 4 and "low" = positions 6; Figure 4.

Species	No. and % of birds perching in the various positions								Totals
	Top		Side arms		Within		Low		
	No.	%	No.	%	No.	%	No.	%	
Tawny Eagle <i>Aquila rapax</i>	1	50	—	—	1	50	—	—	2
African Hawk Eagle <i>Hieraetus fasciatus</i>	1	12	—	—	7	88	—	—	8
Martial Eagle <i>Polemaetus bellicosus</i>	5	83	—	—	1	17	—	—	6
Brown Snake Eagle <i>Circaetus cinereus</i>	6	100	—	—	—	—	—	—	6
Blackbreasted Snake Eagle <i>Circaetus gallicus</i>	46	75	4	7	7	11	4	7	61
Augus Buzzard <i>Buteo augur</i>	1	100	—	—	—	—	—	—	1
Blackshouldered Kite <i>Elanus caeruleus</i>	—	—	—	—	2	100	—	—	2
Pale Chanting Goshawk <i>Melierax canorus</i>	88	67	6	5	33	25	5	4	132
Lanner Falcon <i>Falco biarmicus</i>	2	20	7	70	1	10	—	—	10
Rednecked Falcon <i>Falco chicquera</i>	—	—	1	100	—	—	—	—	1
Rock Kestrel <i>Falco tinnunculus</i>	12	34	—	—	20	57	3	9	35
Greater Kestrel <i>Falco rupicoloides</i>	4	33	1	8	4	33	3	25	12
Totals	166	60	19	7	76	28	15	5	276

ble, therefore, nests should be left in place and undisturbed.

2. The nests of raptors nesting directly above insulators should be left in place until the end of the breeding season. Raptors produce little excreta compared with fish-eating birds and they are unlikely to seriously pollute the insulators in one season. At the end of the breeding season (once the young bird has left the nest) the nest should be carefully moved a minimum distance to an acceptable site on the tower.

3. Sticks hanging down below nests towards conductors should be trimmed without disturbing the main nest structure.

4. Nests containing eggs or young chicks should not be disturbed. In particular, parent birds should not be kept off nests in cold or hot weather as their offspring may chill or overheat and then die.

It is suggested that these recommendations should be made SWAWEC company policy, and all linemen should be made familiar with them.

These recommendations will not only improve transmission line reliability and reduce operating costs, but will also be of benefit to the birds nesting on the tow-

ers, thereby enhancing the conservation image and credibility of SWAWEC in the public mind.

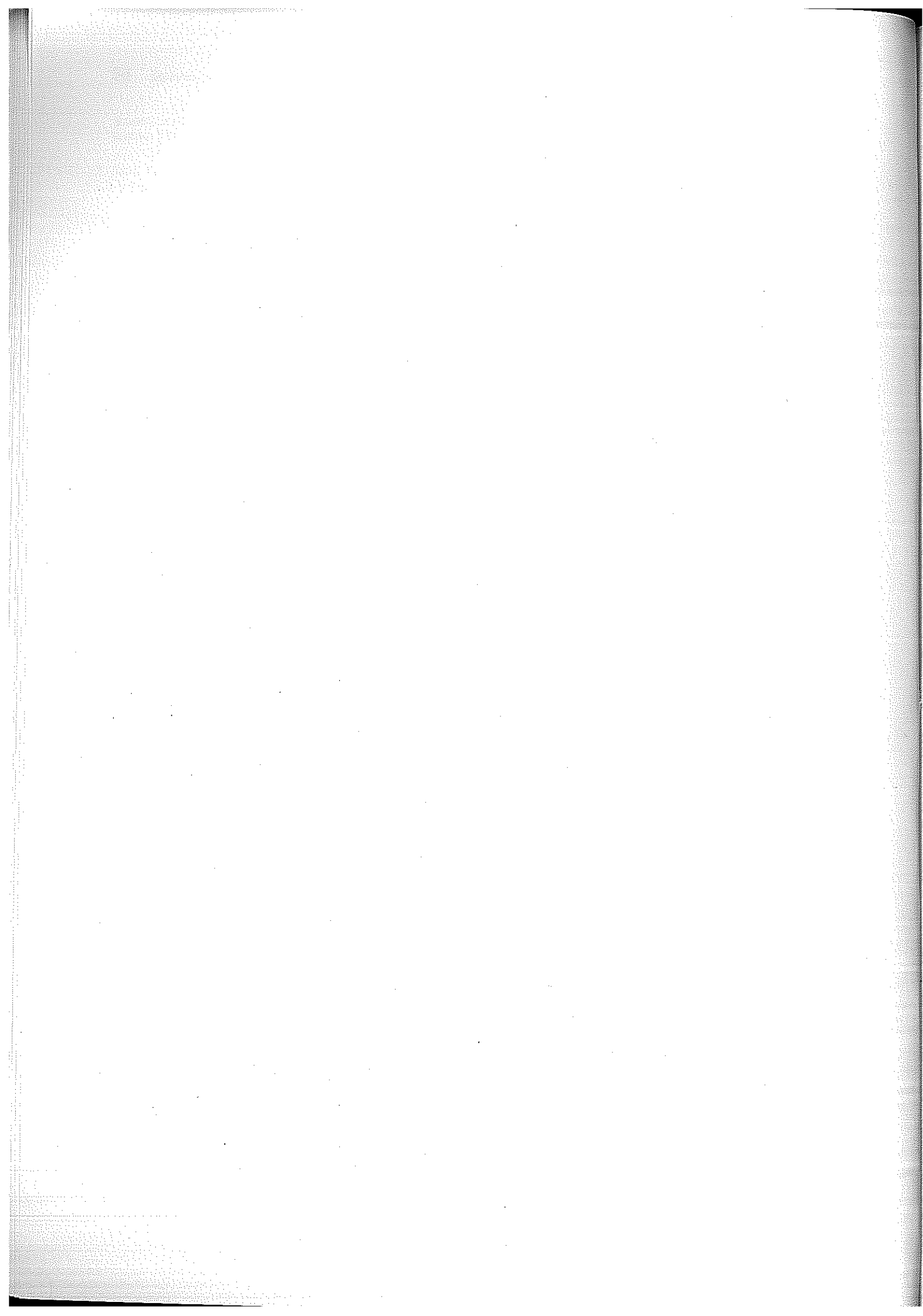
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SHORT NOTE

Some breeding sites of Horus and Bradfield's Swifts
in South West Africa/Namibia

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HORUS SWIFT

The horus swift *Apus horus* is one of three "white rumped swifts" occurring commonly in southern Africa. It has a broad band of white on the rump and a slightly forked tail, differing from the little swift *Apus affinus*, which has a square tail, and the whiterumped swift *Apus caffer*, which has a narrow band of white on the rump and a deeply forked tail.

Whereas whiterumped and little swifts are common throughout South West Africa/Namibia, the horus swift was recorded only in the Eastern Caprivi (Winterbottom 1971; Maclean 1985).

Horus swifts have been recorded over the past few years in small numbers in the Khomas Hochland hills, about 40 km southwest of Windhoek (2216 Dd), e.g. three birds in January 1985 (Brown 1985), two in February, two in March, three in December 1986, three in January 1987 and one in December 1987. Also, two groups of two and four birds respectively were seen in the Otavi Mountains near Kombat (1917 Da) in December 1986.

On 23 March 1986 six horus swifts were seen flying with a flock of about 20 whiterumped swifts at a road culvert about 20 km west of Windhoek (2216 Db). The whiterumped swifts were nesting under the culvert. About 50 m downstream from the culvert the dry river bed had been deeply eroded, forming two parallel, almost vertical earth banks, 200 m long and up to 4 m high. The east-facing bank had a number of deep burrows, excavated by anteating chats *Myrmecocichla formicivora* which were still in residence in two burrows. The horus swifts were swooping past the bank, but once I had moved about 40m away, two birds entered different burrows and a few seconds later two birds left. During the 20 min that I was present, the birds visited four different burrows. I revisited the site three days later and observed the same behaviour.

On 14 May 1988, J.M. Mendelsohn (pers. comm.) observed three horus swifts on the farm Regenstein (2217 Ca) about 10 km south of Windhoek. The swifts visited vertical banks caused by erosion on an alluvial plain. One of the birds, collected for the Windhoek State Museum, was a male with regressed testes (left testis 3×1 mm). According to P.A. Clancey (pers. comm.) the specimen is typical of *Apus horus australis*, the race known to occur in southern Africa in the

southern and eastern Cape, Natal, Mozambique, Transvaal and Zimbabwe (see Clancey 1984).

From these observations I presume that the horus swifts were breeding. Their distribution in this country is more extensive than was previously thought, but they are nowhere common. This is probably because suitable vertical sand and earthen banks are scarce.

BRADFIELD'S SWIFT

Bradfield's swift *Apus bradfieldi* is a largish, uniform mousecoloured swift that ranges widely over South West Africa/Namibia (Winterbottom 1971; Maclean 1985). It is known to breed in horizontal crevices in cliffs (Dean & Jensen 1974; Loutit 1980) and Ryan & Rose (1985) suggested that it might also breed in palm trees.

Bradfield's swift has long been known to roost in the dried fronds of the exotic palm tree *Washingtonia robusta* by residents of this country (14 different sites are known to me) and it has been assumed that they also nested here. In October and November 1986 I was able to confirm this at two sites in Windhoek. Eggs and nestlings of various ages (up to fledging) of Bradfield's swift were found below palm trees that I had been opportunistically watching.

The dead fronds of the *Washingtonia* palm hang down and form a dense mass around the upper stem of the tree. The swifts make tunnels deep into the dead fronds and there build their nests. In the indigenous palms, e.g. *Phoenix reclinata* and *Hyphaene ventricosa*, the dead fronds fall off the trees and thus do not provide suitable nesting sites for Bradfield's swifts. The only other *Apus* swift in Africa known to breed in trees is the black swift *A. barbatus* which breeds in holes in trees in Kenya (Brooke 1971).

Bradfield's swifts were the only birds breeding in the palm trees during these observations, although palm swifts *Cypsiurus parvus*, house sparrows *Passer domesticus* and redheaded finches *Amandina erythrocephala* were also roosting in the dried fronds and all three species subsequently bred there. At one site, consisting of three large palm trees, 18 Bradfield's swifts were estimated to enter the dried fronds in the evening; at the other, seven trees were occupied by about 38 birds. The egg-laying months calculated for

Bradfield's swift at these two Windhoek sites were October and November.

ACKNOWLEDGEMENTS

I thank John Mendelsohn for providing information on the horus swift specimen that he collected and Richard Brooke for his useful comments on an earlier draft of this note.

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SHORT NOTE

Marking and subsequent movement patterns of Springbok lambs in the Etosha National Park, South West Africa/Namibia

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INTRODUCTION

A study of the biology of springbok *Antidorcas marsupialis* began in the Etosha National Park in 1984. We needed to obtain information on age specific mortality and fecundity rates from individually identifiable animals of known age. A primary requirement was to determine a method of tagging which was permanent, visible at a distance and would allow for individual identification for about three years.

Marking animals for identification in research presents a variety of difficulties and is largely dependent on the purpose for making (Taber 1956). Temporary marking has included dyes (Melchior & Iwen 1965), freeze-branding (Farrell 1966), tags, pelage shearing and telemetric devices (Griben *et al.* 1984). Permanent marking has included removal of appendages (Griben *et al.* 1984), branding and freeze-branding (Hadow 1972).

In the present study the priority was that the method of capture and marking be applied quickly and easily to a large number of springbok lambs. This paper describes the methods of marking springbok lambs using ear tags and reports on their local movement patterns during a 24 month period.

METHODS

Capture

All the springbok lambs tagged were captured within 24 h of birth, during the month of January in 1986 and 1987. Springbok lambs tagged were initially captured during the day, by searching an area where springbok herds were seen. Lambs were stalked and caught by hand. Daily captures ranged from 2-8 lambs. Subsequently, lambs were caught at night, when they were easier to find, by means of a spotlight. Hidden lambs were located by the reflection of their eyes. The lambs were weighed, measured, tagged and released within 2 min of capture. Nightly catches ranged from 12-27 lambs.

Marking

Hasco monel metal tags (National Band and Tag Company) with coloured polyvinyl covered nylon straps (Sterkolite) 2,4×4,0 cm were used to mark the lambs. From 1986, tags were attached to both ears to minimise tag loss. One of the tags identified the tagging locality and the other the individual animal.

Research and management personnel in the Park recorded the locations of marked springbok over a 24 month period and tourists provided additional records.

RESULTS AND DISCUSSION

Tagging

During 1985 and 1986, 126 springbok lambs were ear-tagged in four different areas of Etosha (Figures 1-4). Approximately 93% (117) of the lambs were resighted during the monitoring. Eleven lambs were resighted more than once. The numbers tagged in each area are given in Table 1 below.

TABLE 1: Number of male and female springbok lambs tagged during 1985 and 1986.

Location	Males	Females	Total
1985			
Okaukuejo	7	9	16
Namutoni Area	5	-	5
Gemsbokvlakte	-	4	4
1986			
Okaukuejo	19	19	38
Namutoni Area	7	9	16
Gemsbokvlakte	6	7	13
Charisaub Plains	20	14	34
Total	64	62	126

All resighted springbok reported had retained both ear tags.

MOVEMENT PATTERNS

Movements of the springbok lambs during the rainy season February to April and after the rains from May to December are shown in Figures 1-4.

The resightings of the 21 springbok marked in the Namutoni area are shown in Figure 1. Ten (48%) of those marked were within 100 km of the tagging location. The resightings suggests a westerly pattern of movement during the rains.

Figure 2 shows the movement patterns of the 34 springbok marked on the Charitsaub Plains. During the rainy season 29 (85%) were within 50 km of the tagging location while 24 (71%) were within 12 km of the area where they were born.

Of the 54 springbok lambs marked in the Okaukuejo

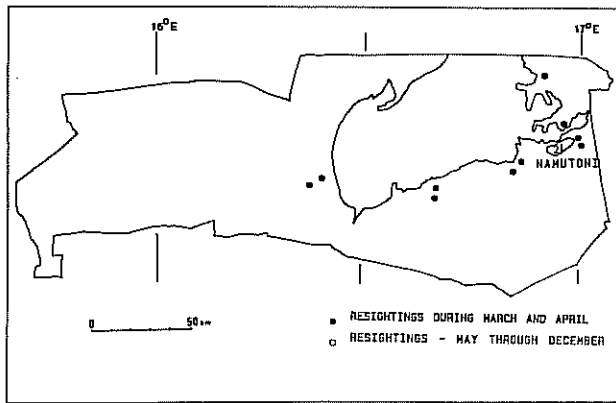


FIGURE 1: Resightings of 21 springbok lambs marked in the Namutoni area during March 1985 and December 1986.

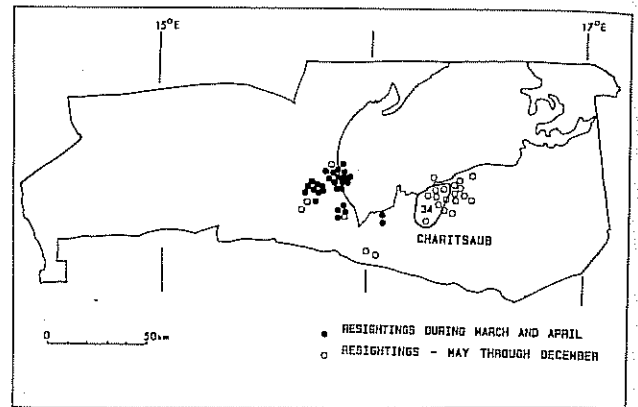


FIGURE 2: Resightings of 34 springbok lambs marked in the Charitsaub area during March 1985 and December 1986.

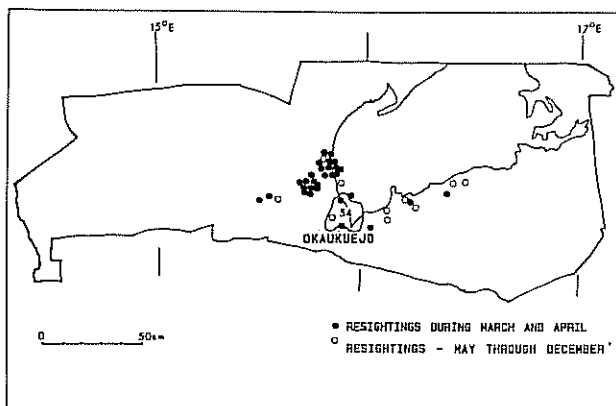


FIGURE 3: Resightings of 54 springbok lambs marked in the Okaukuejo area during March 1985 and December 1986.

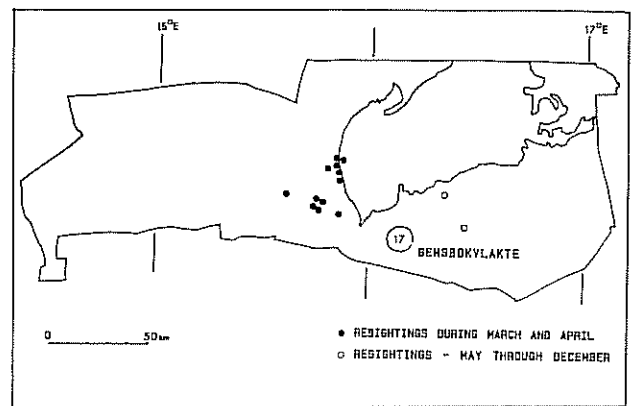


FIGURE 4: Resightings of 17 springbok lambs marked in the Gemsbokvlakte area during March 1985 and December 1986.

area 29 (54%) were within 12 km of the tagging location during the rains and 10 (19%) subsequently (Figure 3). Most springbok marked in this area showed limited movement.

Of the 17 springbok marked in the Gemsbokvlakte area (Figure 4), 12 (71%) were within 50 km of the tagged area at the Okaukuejo plains during the rains. Only 2 (12%) were within 20 km of the tagged area after the rains. Thus, the animals born in this area moved to the adjacent plains areas where grazing may have been more attractive.

INDIVIDUAL MOVEMENTS

Individual movements of eight springbok lambs are given below (Table 2). Distance moved by marked springbok ranged from 1–80 km between the tagging and resighting locations. Two males moved more than 80 km's, one marked in the Charitsaub plains and resighted north of Okaukuejo some 60 days later, the other tagged in the Okaukuejo area and resighted 60 days later at Okondeka. This second lamb was resighted at the Charitsaub plains 20 days later, having moved a farther 80 km.

The movement of springbok lambs for the first 12 months after birth seems localised. The lambs remain in the general area where they were born. The one ex-

TABLE 2: Location of eight marked and resighted springbok lambs giving approximate distances moved.

Marked		Resighted		Approx. Distance (km)
Area	Date	Area	Date	
Charitsaub	10/1/86	Charitsaub	1/5/86	1
Gemsbokvlakte	13/1/86	Charitsaub	1/5/86	37
Charitsaub	14/1/86	Charitsaub	1/5/86	1
Charitsaub	14/1/86	Charitsaub	1/5/86	1
Charitsaub	14/1/86	Okondeka	22/4/86	80
Okaukuejo	15/1/86	Okondeka	10/4/86	28
		Charitsaub	1/5/86	80
Gemsbokvlakte	15/1/86	Leeubron	16/2/86	55
Okaukuejo	17/1/86	Okaukuejo	30/4/86	1

ception was the springbok in the Namutoni area, which moved westwards to better grazing. The boundary fence in the Namutoni area restricts movement further to the east and may result in the animals returning to the plains in the west. Based on total game counts in the plains areas of Etosha, Grobler (1978) stated that an extensive easterly pattern of movement seemed to occur, with springbok moving on the plains skirting the Etosha Pan in the direction of Namutoni. This pattern of movement seems to have changed during the period since 1978 possible because of different rainfall patterns in the area. The present

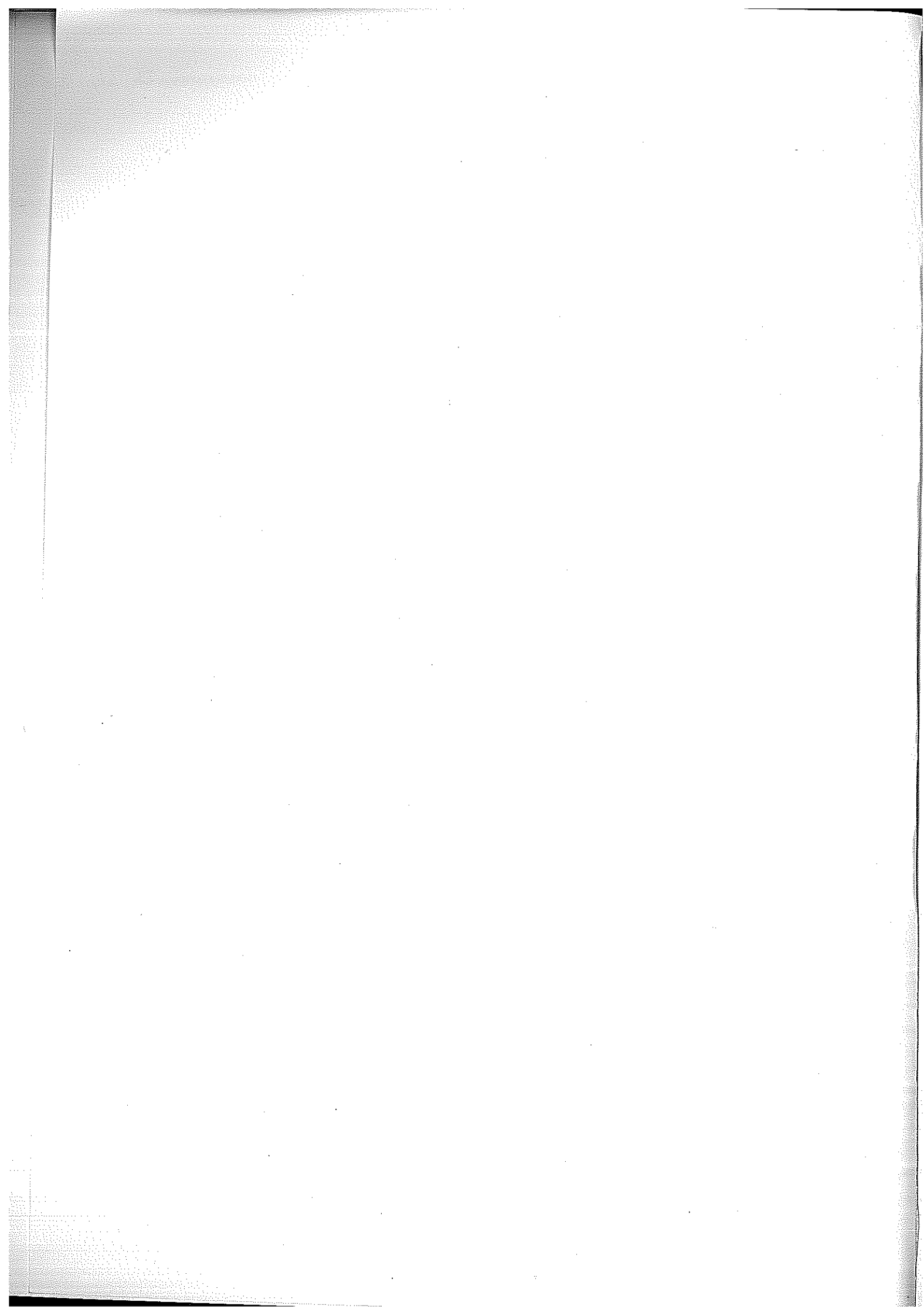
study suggests limited movement by springbok. Movement patterns seem to be determined by the amount of green grass available, with adult springbok and their young moving to the improved grazing areas. In a study in the Western Transvaal Van Zyl (1965) found that grass was the most important food item of springbok during the rainy season followed by shrubs in the dry season, possible because the nutritional value of grass is important only when green, whereas shrubs retain much of their food value throughout the year (Leistner 1967). The movement of springbok in Etosha appears to be determined by the amount of green grass present in the areas where they are born. The lambs move with their mothers to the nearest plain areas as the grass begins to dry.

ACKNOWLEDGEMENTS

We thank all the personnel in the Park for their help and for making their observations available.

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SHORT NOTE

Probable visible migration of Grey Plovers *Pluvialis squatarola* at Swakopmund, South West Africa/Namibia

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Between 19h05 and 19h15 on 8 April 1988, I observed, from the pier at Swakopmund, six flocks of grey plovers *Pluvialis squatarola*, totally c. 1000 birds, flying northwards. The flocks were flying parallel to the shore, c. 50 m from the beach at a height of c. 10 m. Each flock veered and rose slightly as it rounded the end of the pier. No further flocks were observed between 19h15 and 19h30.

Sandwich Harbour and Walvis Bay Lagoon are two major wetlands for waders, 40 km and 80 km to the south, respectively (Whitelaw *et al.* 1978). If these flocks were on migration, it is possible that they departed from either of these two wetlands shortly before sunset (18h45). I had observed grey plovers in near-complete breeding plumage at Walvis Bay Lagoon earlier on the same day, and at Langebaan Lagoon in the southwestern Cape three weeks earlier on 19 March 1988. Tarr & Tarr (1987) observed that densities of grey plover on the northern Skeleton Coast were highest in October and April, indicating that these are the peak months of southwards and northwards migration, respectively.

Grey plovers ringed in southern Africa have been recovered in northern Italy, Romania and the Crimean region of the U.S.S.R. This suggests that at least part of the population migrates along the east Atlantic coastline to the Gulf of Guinea, across the Sahara to the eastern Mediterranean and the Middle East, and on to their assumed breeding grounds in the Taimyr Peninsula (SAFRING unpubl. data). This route is close to the Great Circle linking southwestern Africa and the Taimyr Peninsula. Thus Swakopmund lies along a migration route for grey plovers.

There are no important feeding areas for grey plovers along the coast immediately to the north of Swakopmund to which these birds could have been flying (Un-

derhill & Whitelaw 1977). However, an alternative explanation for the movement of birds past Swakopmund at dusk is that they were *en route* to the salt works 5 km north of Swakopmund to roost overnight. This seems unlikely because there are also saltworks at Walvis Bay Lagoon at which they could roost.

Whether these particular birds were on migration or not, the pier at Swakopmund might prove to be strategic observation point for visible migration. If waders do tend to set out on migration from nearby wetlands at about sunset, they would pass Swakopmund before nightfall. Radar studies, such as those conducted by Grimes (1974) and Grimes and Vanderstichelen (1974) in Ghana, would also be valuable in observing migration along this section of coastline.

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MENDELSSOHN, H. & LESHEM, Y. 1983. The status and conservation of vultures in Israel. In: WILBUR, S.R. & JACKSON, J.A. (eds.). Vulture biology and management. Berkeley: University of California Press: 86-98.

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VOLUME 16 · NUMBER 1

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CONTENTS INHOUD

Channing, A. New frog records from the Eastern Caprivi Strip, South West Africa/Namibia.....	1-4
Ferreira, J.T. On the inheritance of the red colour in the Mozambique Tilapia <i>Oreochromis mossambicus</i>	5-8
Ferguson, J.W.H. Summer activity patterns of the riparian desert beetle <i>Physadesmia globosa</i>	9-13
Tarr, P.W. & Tarr, J.G. Veld dynamics and utilisation of vegetation by herbivores on the Ganias Flats, Skeleton Coast Park, SWA/Namibia	15-22
Rebello, A.G., Holmes, P.M., Hilton-Taylor, C., Samper, C., Knight, R.S., Kurtzweil, H. & Bapst, P. Branching patterns in <i>Aloe dichotoma</i> - is <i>A. ramosissima</i> a separate species?	23-26
Van Vuuren, N.G., Mulder, P.F.S., Ferreira, J.T. & van der Bank, F.H. The identification of hybrids of <i>Barbus aeneus</i> X <i>B. kimberleyensis</i> and <i>Labeo capensis</i> X <i>L. umbratus</i> in Hardap Dam, SWA/Namibia	27-34
Lizemore, E., Ferreira, J.T. & van der Bank, F.H. An electrophoretic and morphometric evaluation of the two subspecies of <i>Tilapia rendalli</i> from southern Africa	35-39
Herzig-Straschil, B. & Herzig, A. Biology of <i>Xerus princeps</i> (Rodentia, Sciuridae)	41-46
Braine, S. Range extensions, food and breeding of the Marsh Owl in the northwestern Namib, South West Africa/Namibia	47-49
Boyer, D.C. & Boyer, H.J. The status of alien invasive plants in the major rivers of the Namib Naukluft Park	51-58
Brown, C.J. & Lawson, J.L. Birds and electricity transmission lines in South West Africa/Namibia	59-67
SHORT NOTES:	
Brown, C.J. Some breeding sites of Horus and Bradfield's Swifts in South West Africa/Namibia	69-70
Panagis, K. & Stander, P.E. Marking and subsequent movement patterns of Springbok lambs in the Etosha National Park, SWA/Namibia	71-73
Underhill, L.G. Probable visible migration of Grey Plovers <i>Pluvialis squatarola</i> at Swakopmund, SWA/Namibia	75

