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Structure and pattern of the Namib Desert dune ecosystem at Gobabeb

by

E. Holm and C. H. Scholtz
University of Pretoria, Pretoria

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ABSTRACT

Composition and patterns of the main biotic and abiotic components of the system are outlined. Notes on biology and ecology of 137 recorded animal species are given, with special attention to the aperious arthropods which dominate the system. The results of a one-year trapping survey are used to illustrate habitat preferences, diet activity cycles and seasonal occurrences of the majority of the species. Endemism and geographical distribution of the beetle fauna are discussed. Illustrations include a site map; histograms of trapping results against yearly and daily climate and against habitat; photographs of a selection of the arthropods; and distribution maps of most of the recorded beetle species.
1 INTRODUCTION

This paper is primarily intended as a field guide to the Namib Desert dune ecosystem in the area south of Gobabeb. The unique ecology of the Namib dunes has attracted researchers from across the world to the research station at Gobabeb. A field guide for scientists to the general ecological pattern of the system is long overdue.

We have condensed data which one of us (E. H.) collected during a three-year stay at Gobabeb (1967 – 1970), and which was previously only available as an unpublished MSc thesis of the University of Pretoria. We also added records and notes of four subsequent expeditions into the central Namib which we did under the auspices of the University of Pretoria. The results presented here cover a wide field, and are not intended to compare with those of the many excellent specialised studies done at Gobabeb since the early 1960’s. Our references were selected to serve as background and introduction to specialised fields of research, and not as a comprehensive bibliography on Namib research.

2 METHODS

2.1 Trapping

The trapping survey on which most of the present paper is based was done during 1969, with a preliminary trial run in 1968. The traps were fully described by Holm & Edney (1973) and the problems encountered with statistical analyses of the results are discussed in the same paper.

The results in Figs 2, 3 and 4 are based on catches of nine of these unbaited pit traps, four of which were fitted with mechanisms to separate 2,2-hourly catches, given in Fig. 3. Trap No. 1 was placed on an east-facing dune slip face, and was fed by a flat funnel with the same circumference as the other traps. This trap filled up with sand with every strong wind, and could not follow the leeward slip-face with change in wind direction as the fauna does. As the whole insect activity on the dune crest is concentrated on the slip-face, and activity increases with wind velocity, this trap undersampled the dune crest fauna to an extent that made only qualitative sampling possible. Trap No. 8 was installed three months after the others, while trap No. 3 was also prone to fill up with sand. The remaining six traps were non-functional for between 15 and 20 days during 1969, but not necessarily on the same days.

We have multiplied the catches of traps 1, 3 and 8 with factors to bring them on a par with the average 18 missed trapping days of the other traps for Fig. 4. It is appreciated that this crude procedure could not compensate for the probably very heterogeneous missed catches on different days in the yearly cycle, and this circumstance made further statistical analyses of the data meaningless. Similarly, daily trappings in Fig. 2 were corrected for the number of non-functional traps for any given day, but because of the spatial heterogeneity of trapping sites, these corrections did little to improve the statistical reliability of the data. The average error in the data is 258 missed trap-days, or about 10% of the possible trap-days. Data on strictly seasonal species will be affected most.

The timed catches given in Fig. 3 are affected in some cases by the relative abilities of the different species to jump from one tin to the other (which, again, depended on the sand level within the tins). Thus Nos. 21 and 22 are known to be strictly diurnal, and the night catches are due to this error in these very active species. In other cases, a few odd catches may be attributed to disturbed specimens or specimens with disorientated cycles (e.g. No. 136).

Most trapped animals were marked with paint and released near the traps. Only in exceptional cases were animals removed for identification.

The animals of the dune fauna have a poorly developed sense of vertigo as would be expected in a natural surrounding which lacks sharp precipices. Pit trapping is therefore very successful in the dunes, and observations have shown that at least the diurnal species run straight into the traps without hesitating. There is a possibility that animals were attracted to the traps by the smell of others already in the traps, but the funnel-lids and the fact that traps were emptied daily (between 10h00 – 10h30) would have limited this to a minimum. On a few occasions when the flooded Kuiseb River prevented access to the traps, they were not serviced for several days. On these occasions animals died in the traps and olfactory attraction could have considered enhanced catches. For other days, as in Fig. 2, as well as in Figs 3 and 4, attraction would be rather similar for the various traps or time segments.

The trapping results obviously do not reflect densities, but rather densities x activity of the various species. Since activity is closely correlated with energy turnover, the results may be used as a crude indication of ecological dominance. The nine traps were placed in such a way that their own surface areas were roughly proportionate to the surface area of the various habitats of the study site (i.e. more traps were placed in the larger habitats) and apart from the dune crest fauna which was undersampled, due to the failure of trap No. 1, the trapping results are probably a fair reflection of the relative ecological dominance of the various species.

2.2 Observations

A few intensive surveys of animal activity (see Holm & Edney 1973) and many hours of observation during the servicing of traps, field work on other projects and collecting expeditions, were used in our discussions and interpretations.
FIGURE 1: Map of the study area and surroundings indicating elevations, geomorphology and the distribution of vegetation.
2.3 Distribution survey

Data on distribution were gathered on four expeditions from 1975 to 1978 (Fig. 8). These expeditions were done with post graduate and senior undergraduate students, and sampling was mostly done for 24 hours in an ½° block. The collected material was preserved and identified, and other records housed in the two major collections of Namib beetles, i.e. the Transvaal Museum and the Windhoek State Museum, were added to our own. Distribution limits of species which extend outside the central Namib are mainly based on material in these two collections. Only the beetle distribution is mapped, since material of other groups was not intensively collected and was disseminated to various specialist taxonomists. Only the distribution of beetles occurring in the study area is given, the distribution of other species of the Namib will be given and discussed elsewhere.

3 PHYSICAL ENVIRONMENT

3.1 Substrate

The study site is situated at S 23°37' E 15°01', and at a basal altitude of 400 m above sea level (Fig. 1). It is situated centrally in the Namib Desert, which may be divided into four major biotopes:

3.1.1 The sub-desert (often called the 'pro-Namib') forms a transition between the semi-arid Namaqualand mountains in the south and Khomas Hochland mountains in the west, and the coastal strip of the Namib proper. In the southern coastal area this biome extends with little change up to the Cape Peninsula, and the coastal Namaqualand should probably be included in the Namib rather than the Karoo. In the far south, and north of the Khomas Hochland, the sub-desert becomes ill-defined and grades into the desert plains and coastal dunes.

3.1.2 Extensive desert plains occur north and south of the central Namib dune-sea, and isolated smaller plains occur within all dune areas and between individual dunes. These plains are characterised by the lack of vegetation except in the short periods following the isolated and sporadic rain showers in the desert. Where the sub-desert plains mostly have vegetation and consist of stabilised dune sands mixed and interspersed with gravel and rock outcrops, the desert plains are barren gravel and coarse sand, underlain by gypsium dust with a high salinity, often with salt crusts at or near the surface.

3.1.3 Savanna and Namaqualand enclaves occur on rock outcrops and along river-beds in the desert. Rock outcrops occur throughout the sub-desert, desert plains and dune areas. Their height and position from east to west determine the degree of aridity but all are characterised by succulent vegetation and inland and sub-desert faunal elements. The dry river-beds or 'wadis' support a more definite savanna fauna and flora, which is gradually replaced by more hardy desert forms on the gradient of desertification from east to west. Where river-beds have rocky banks, their communities are very similar to those of inselbergs at the same longitude.

3.1.4 Large dune areas occur between the Aus-Lüderitz and Kuiseb Canyon-Walvis Bay lines in the south, and on the north coast of South West Africa up to Moçamedes in Angola in the north. Scattered dunes and small dune fields occur around the lower Orange River, between Lüderitz and Elizabeth Bay, between Walvis Bay and Swakopmund, and north of the Ugab River on the Skeleton Coast. The two large dune fields have led to a distinction between northern and southern Namib. Faunistically it is more appropriate to distinguish between a southern area (south of Lüderitz), a central area and a northern area (north of Walvis Bay).

The present study is concerned with the central dune area and inter-dune plains, and in particular with the area directly south of Gobabeb (about halfway between the vegetationless coastal dunes and the semi-stable and largely overgrown inland dunes). The dunes in this area, as in most of the central Namib, are linear dunes with barchanoid ridges and with an average height of about 100 m above the inter-dune plains, and are oriented in more or less continuous north—south ranges. In the study area the fauna is not purely of the dune biotope, since many species of the Kuiseb river-bed enter the adjacent dune area marginally or opportunistically, creating an ecotonal diversity.

On a smaller scale the study area may be further sub-divided into four fairly discrete substrate types (Fig. 1):

(i) The plains between dune ranges (or interdunes) are like the large desert plains described above, but have a higher content of dune sand in the surface pebble layer. In the study area the bed-rock surfaces in small areas, and in the south a terrace of consolidated dune sand and pebbles of alluvial origin replaces the plains.

(ii) The dune foot (or base) is a distinct area at the transition from plains to dune slope, and is characterised by coarse white quartz sand at the surface and the formation of regular ripples of micro-dunes which vary between a few centimetres and half a metre high. This area has a few species which specialise in using the detritus precipitated in these micro-dunes (e.g. No. 110). The relative stability of the coarse sand allows for short-lived vegetation to grow after rains, and dune slope species and plains species overlap here.

(iii) The dune slopes (or plinths) cover the largest surface area of the dunes and consist of moderately fine and compacted sand. This area has most of the perennial vegetation, and the hummocks of sand precipitated around these plants are the centres of animal activity on the dune slopes. The plant hummocks provide shelter from heat, protection from predators and food and moisture (see peren-
nial vegetation below). Very few animals feed on the plants themselves.

An important feature of the dune slopes is the retention of moisture in the sand (see Holm & Edney 1973) and the cohesion of sand grains at night, which make this area most suitable for tunnelling. The cohesion of the sand particles is an involved phenomenon, dependent on i.a. temperature and moisture, and even at relative humidities of 50% or lower the surface becomes firm enough for tunnelling in the sand at night. At sunrise the dune slopes are studded with tunnels of all sizes but with rising temperature the entrances collapse, soon leaving no trace of fossorial activity on the surface.

The valleys between dune crests above the slopes are similar to the slopes in vegetation and faunal composition. The sand is softer and finer in these troughs, perennial plants more abundant and detritus precipitation probably higher due to wind breaks on all sides. Most dune slope species are more abundant in these valleys than on the exposed slopes.

(iv) The dune crest system consists of the actual crest, the slip-face of loose sand which is formed by precipitation of sand on the leeward side of the crest and the base of this slip-face (or avalanche base) where it meets the firm dune slope. On the windward side the crest may be so firm depending on how long the winds have blown in the same direction, and with a change in wind direction the whole system gradually changes over to the other side. As the wind pattern is strongly seasonal (Fig. 2), slip-faces face predominantly east in summer and sporadically change to west in winter. The fauna of the slip-face are all sand-divers, and with change in wind direction change over to the leeward side where the sand is loose, wind force is low and detritus precipitation is highest of all areas in the dunes.

Wind-blown detritus and airborne sand are precipitated on the leeward slip faces by the leeward vacuum created by the barchan-type crests. This detritus then swirls on the slip-face and accumulates in cushions in the wind-still spots, and the small detritivores use the same eddies to transport them to the food. Unconsumed detritus becomes submerged by sand, and is eventually utilised by tenebrionid larvae, Thysanura and probably some of the adult tenebrionids. Heavier particles of detritus collect at the slip-face base, where species or both the dune slope and slip-face may be found browsing amongst them.

The sand of the slip-face is of very homogeneous grain size, and the grains are smoothly polished. On a set of imperial measure soil sieves a 1 kg sample from a dune crest gave the following breakdown:

- retained on 30 meshes/inch: —
- retained on 50 meshes/inch: 14%
- retained on 100 meshes/inch: 81%
- retained on 200 meshes/inch: 5%
- passed through 200 meshes/inch: 0.01%

The smoothness of grains and absence of dust are essential for the sand-diving insects, as is demonstrated by the effect of placing them in ordinary building sand. The beetles soon wear their appendages down to stumps. More information on the properties of dune sand in relation to the psammoophilous animals is given by Robinson & Seely (in prep.).

The dune crest never supports any vegetation. The only protection from heat is the steep 32° angle which affords shade for a few hours every day and the loose sand which permits sand-diving. The dune crest community and food chain are dependent on wind-blown detritus as basic energy source.

Several authors have given general descriptions of the geomorphology of the area (e.g. Koch 1961, Kühnelt 1969, Coetzee 1969, Seely 1978c) and many more detailed and specialised analyses of aspects of geomorphology and geology of the central Namib have been published recently (Barnard 1973; Besler 1970, 1972, 1975a, 1975b, 1976; Goudie 1970, 1972; Logan 1972; Nagtegaal 1973; Rust 1975; Schoz 1973; Selby 1976; Wieneke & Rust 1973, 1976). A fuller description of the dune environment will be given by Robinson & Seely (in prep.).

3.2 Climate

The climate data given in this paper are all from the First Order weather station of the South African Weather Bureau at Gobabeb, about 1.5 km NW of the study site.

3.2.1 Wind is ecologically the most important factor in the system. Not only is the structure and texture of the substrate largely determined by wind action (see 'substrate' above), but the wind regime also controls the temperatures and humidities, distributes the basic energy source (detritus) and determines modes of locomotion of the arthropods. The general annual regime is fairly predictable and more or less conforms with the pattern recorded for 1969 (Fig. 2). In summer the winds are mainly westerly and stable, rarely reaching gale strength but also with few calms. Cool and moist sea air is brought in by these westerly winds, but occasional north winds may be hot and dry. In winter regular spells of east winds alternate with periods of calm or moderate westerly winds. These easterly ‘berg’ winds reach high velocities at about two-weekly intervals, and spells of east wind are marked by high temperature maxima and humidities as low as 0 – 5% RH due to an air drop of about a thousand metres from the Khoras Hochland escarpment. Easterly storms usually set in before dawn, reach a peak at
noon and subside before sunset, at the same time rotating from SE through E to NE.

3.2.2 Temperatures are highly dependent on wind direction and the short east wind spells in winter cause the average maximum temperatures for summer (32°C) and winter (27°C), and the average minimum temperatures for summer (15°C) and winter (10°C) to differ by only 5°C. Highest maximum temperatures are above 40°C in summer and about 35°C in winter, with an absolute high of 42°C between 1960 and 1970. Although the macroclimatic temperature conditions are therefore hardly extreme in the Namib compared to inland deserts such as the Kalahari, temperatures may change very rapidly with change in wind direction. Changes of up to 15°C in maximum or minimum temperature within a matter of days are common, and temperature changes of the same magnitude may occur within hours on a given day. It must further be borne in mind that the dune environment offers little shade, and surface temperatures of above 70°C are recorded for screen temperatures below 40°C. On the red north-facing dune slopes, surface temperatures would undoubtedly be even higher. Frost was never noted at Gobabeb, although surface minimum temperatures below 0°C were recorded.

3.2.3 Humidities at Gobabeb vary widely, are usually negatively correlated with temperature and also wind-controlled. The lowest humidities (0 – 5% RH) occur with easterly storms, and noon humidities are rarely above 50% RH. Daily averages are about 60% RH for summer and 35% RH for winter. In summer saturation is often reached when advective sea fog covers the area in the early mornings. Fog precipitation is highest in spring but may occur throughout the year, mostly between midnight and 0800 (Fig. 2). The average fog precipitation is 30 mm p.a., which is more than the average rainfall of about 25 mm p.a.

Rainfall was exceptionally high in 1969, with 66 mm recorded in a two-month period. These rains produced an exceptionally good cover of annual vegetation, which was completely absent in 1968 when less than 20 mm rain was recorded (Fig. 2). Rainfall is apparently bimodal, with the highest probability for occurrence in late summer. Showers are extremely localised, resulting in sharp-edged patches of grasslands.

For those arthropods which are directly dependent on water, the amount of precipitation is less crucial than the frequency. When occurrences of rain, fog and dew are added, the maximum spell between precipitation of some kind was about 2 weeks in 1969. Fog occurrences and utilisation by the arthropods are discussed by Seely (1979).

Evaporation is about 3 500 mm p.a., which is not much higher than in the inland savanna, e.g. at Windhoek. In the central Namib most of the evaporation takes place in winter during east wind spells, while evaporation is highest in summer in the inland.

The macroclimate at Gobabeb was first analysed by Schulze (1969), and a further summary was provided by Seely & Stuart (1976). Further discussions of the climate were given by Goudie (1972), Besler (1972), Seely (1978c) and Robinson & Seely (in prep.), while many of the papers dealing with geohistory and geomorphology contain information on the present and past climate (see references under "substrate" above). Microclimatic data were given in many of the papers on behaviour and physiology of the invertebrate and small vertebrate fauna (e.g. Edney 1971; Hamilton 1971, 1973, 1975; Hamilton & Seely 1976a, 1976b; Henwood 1975a, 1975b; Hoim & Edney 1973; Kühnelt 1969; Louw 1972, Louw & Hamilton 1972; Seely & Hamilton 1976; Seely (in press), and a summary of microclimate may be found in Robinson & Seely (in prep.).

4 THE VEGETATION AND ITS ECOLOGICAL ROLE

Ecologically, plants in the study area fall into two distinct groups, the first comprising the larger perennial plants and the second the small and short-lived annuals which only appear after sufficient rain.

The perennials consist of three species. Stipagrostis sabulicola (Pilger) de Winter, a hard and spiny dune grass which grows to over one metre in height, is the dominant species of this group on the dune slopes. Normally there is little green growth on the tussocks, and most growth takes place after rain. As discussed above, the most important ecological role of these plants is providing shelter and a modified substrate, and for the precipitation of wind-blown detritus and fog. In periods of slow growth, only the root pseudococcal (No. 62), an undescribed agrilene stem-boring buprestid (which was not recorded in the study area) and a lepidopteran (Wharton, pers. comm.) are known to feed on the grass. After rains the green grass is eaten by the oryx, several curculionids (Nos. 101–103), locusts and grasshoppers, tenebrionids and aphids (the latter was also not recorded during the survey). The inflorescences are frequented by the buprestid (No. 96), and two Onymacris spp. (Nos. 133 and 134) have acquired the technique of climbing up the stems to feed on the ripe seed of the grasses. Dead growth and the remainder of the seed eventually enter into the detritus pool.

Acanthosicyos hordrida Welw., the narra plant, is a spiny semi-succulent, evergreen cucurbit shrub. Large plants may grow to about one metre tall and may sprawl over hummocks of up to ten metres in diameter. The ecological role is similar to that of Seely (1979). and here too very little vegetative tissue is used by consumers. The yellow flowers are eaten by the meloid (No. 94) and the buprestid (No. 96) and are visited by a variety of wasps and flies. When the flowers drop off, O. plana and probably other scavengers feed on them (Seely, pers. comm.). The fruits,
which are commercially harvested in the lower Kuiseb, are round and spiny, with a diameter of about 100 – 150 mm. They are favoured by the oryx, and once broken the succulent flesh and seeds attract a variety of arthropods. The seeds constitute a high percentage of the diet of the gerbils (No. 3) when available, and are also sought out by those tenebriionids which can break the shells with their mandibles, and also by the narra “cricket” (No. 52).

The narra seems to require dune sand and subterranean water, and may be a useful indicator of water. It only grows near river-beds or former river-beds, e.g. the lower Kuiseb delta and the underground course of the Keichab. In the latter case where valleys full of narra plants were observed in 1977 to have died, presumably due to pumping operations in Keichab pan and a subsequent drop in the water table. At the Uri Hauchab mountain in the dunes, the only narra plants grow above the subterranean lower course of a fountain. Large stands of narra also occur SW of Gobabeb in the dunes, probably on subterranean branches of the Kuiseb-Tsondab system. In the study area the plants grow on lower dune slopes near the Kuiseb River, and become progressively smaller and scarcer towards the south.

*Trisanthema hereroensis* Schinz is a non-spiny succulent cushion plant which grows on the higher dune slopes and in valleys on the dunes. Although the plant is evergreen and very succulent, it is not usually eaten, except after rains when two weevils (Nos. 99 and 103) and several lepidopterous larvae (Wharton, pers. comm.) feed on it (see Fig. 4). Flowers are small, and attract a variety of flies and wasps. Salticid spiders are commonly found in flowering plants. Of the three perennials in the area, *T. hereroensis* is the only species which extends into the mobile coastal dunes where not even short-lived annuals can grow.

The rain dependent annuals only appear after rains of above 20 mm within a short period, as was e.g. recorded at Gobabeb in 1967 and 1969*. In 1968, when only 10 mm was recorded, they were completely absent. Small grasses, mainly *Stipagrostis* spp. (e.g. *S. gonastostachys*), predominate in this group, which otherwise consists of a few lilies (e.g. *Hexaeris diekiana*) and one small dichotomous plant with a deep root-bulb, *Monsonia ignorata* Merxm. & Schreiber. The annuals can only take root on the relatively stable sands of the lower dune slopes and plains (Fig. 1). The growth of a dense cover of grasses is followed by a well synchronised emergence of a great variety of arthropod primary feeders, which reach extremely high population densities followed by equally dramatic population ‘crashes’ after a few weeks when the plants have died. Densities of *Eustolopus octosieratus* (No. 130) reached such high levels in 1967 that it was impossible to walk in the plains without continually stepping on these beetles.

The annuals also attract perennials from the sub-desert and savanna, such as large herbivores and associated dung beetles, mammalian and avian predators and alate insects. The rain-flora thus supports a whole short-lived ecosystem within the permanent detritus-based system, and the frequency of its occurrence for any given spot is about once in three years at the longitude of Gobabeb, probably becoming more frequent towards the east and less frequent towards the coast. This would necessitate prolonged quiescences for the arthropod consumers which specialise on the rain-flora. The grasses last for about one month after rains (depending on weather conditions), and the lilies and *Monsonia* sp. outlast grasses by a few weeks. The food supply is so short-lived that it is not overtaken by primary feeders and the bulk is uprooted by wind and changing sand-surface levels, and is eventually distributed through the dune area as probably the major part of the detritus deposits (Robinson & Seely, in prep.).

Apart from intensive studies on *Welwitschia mirabilis* (which does not occur in the study area), few of the plants of the central Namib have been intensively studied. Giess (1962, 1968), Walter (1962) and Robinson (1976) recorded the floristics of the area, and Herre (1974/1975), Walter (1976) and Seely, de Vos & Louw (1977) published ecological observations on some of the plants. Seely (1978a, b) analysed the productivity of the annuals in relation to rainfall and included useful check-lists of species compositions.

5 CONSUMERS: VERTEBRATES

Since this study was mainly concerned with the endemic arthropods, our less detailed notes on the vertebrates are given in this separate chapter. Information from the extensive literature on vertebrates of the Namib is not repeated or quoted as this would be beyond the scope of the study, and selected references are provided instead.

5.1 Primary feeders

Species recorded in the study area are the oryx, *Oryx gazella* (No. 1) and hare, *Lepus capensis* (No. 2) (see Dixon, 1975), both of which are migrants from the overgrown inland dunes and sub-desert. Both species were rare in the study area and the wingless scarabs (Nos. 87 and 88) which usually occur with them, were also rarely trapped. Some omnivorous species contribute to primary consumption, and these are discussed elsewhere. Even normally carnivorous species e.g. the spotted hyena (Stuart 1976) and certain geckos and lizards (see below) eat vegetable matter on occasions. Ostriches were sighted in the area on one occasion, but do not usually enter the dunes. Granivorous birds invade the area when seed is plentiful, but are not resident in the dunes.

*Seely (1978a) independently arrived at a figure of 20.6 mm.*
5.2 Larger predators

These include the jackal, Canis mesomelas (No. 5), the brown hyaena, Hydrooa brunnea (No. 6) and several snakes and birds of prey. All feed mainly on arthropods, but also take smaller mammals, reptiles and birds.

The jackal is quite abundant in the dune area, and reaches particularly high densities along the coast. Tracks following those of gerbils and moles were often seen in the mornings, and droppings contained many arthropods shells (see also Stuart 1976).

The brown hyaena (No. 6) is rare in the area, and apart from two sightings, the only tracks of this animal were seen during 1969. Only recently the spotted hyaena has been seen near Gobabeb, and it is possible that the brown hyaena is disappearing in this area.

Two species of grass snakes were observed in the area. The most common species, Psammophis leightoni namibensis (No. 8) was often found in hummocks of perennials at the dune foot, and two instances of predation on Merolea sp. (No. 14) were witnessed in the study area. The other species, P. notosilicis was seen in the study area once. A review of the two species was given by Brodeley (1975).

The sidewinding adder, Bitis peringueyi (No. 7) is one of the best adapted desert vertebrates of the Namib. It has a mode of locomotion similar to that of the unrelated American sidewinders (Gans & Mendelsohn 1971) and several other behavioural and morphological adaptations to the dune environment. The eyes are situated on top of the head, which is cryptically coloured like the rest of the body. The snake submerges itself in dune sand by moving the ribs sideways until only the top of the head is exposed. It is in this position that it lies waiting for prey. The snake's tail is thin, and is black in some specimens. A specimen which one of us (E. H.) held in captivity at Gobabeb, used this black tail tip successfully as a lure to attract Aporosaura (No 13) specimens in the cage by wriggling it above the sand surface. The behaviour was observed repeatedly on this specimen, but this lure is apparently not always employed. At night the snakes roam over the dunes in the characteristic sidewinding fashion, and probably hunt Palmatogecko (No. 12).

A further interesting observation was made on a captive snake which had been exposed to desiccation and was subsequently sprinkled with water. The snake immediately coiled with the head in a central position and flattened the fore-body, thus forming a funnel with its body to channelise the water to the mouth (see also Louw 1972 and Robinson & Hughes 1978). In the dunes, a specimen was once found at noon in a tussock of Eragositis spinosa grass. On this particularly hot day the snake apparently took refuge from the intolerable surface temperature by climbing into the plant. The sidewinder is very common in the study area and throughout the central Namib dunes. Six specimens were trapped in pit traps, all between mid-August and November, while there was a period of three months in winter in which activity declined sharply and no snakes were seen (Fig. 2). All specimens were trapped on the dune slopes and crest (Fig. 4). The biology of the species was recently described by Robinson & Hughes (1978).

Important larger avian predators in the dunes are the pied crow (No. 20), the owls (Nos. 18 and 19) and the goshawk (No. 17). These species all take small vertebrates as well as arthropods. The crows and goshawks are often seen on dune crests, watching the slip-face for movement and then striking at beetles or lizards. The diet of the owls has been extensively studied by examination of pellets (Bauer & Niethammer 1959; Nel 1969; Stuart 1975), and while it consists mainly of small mammals, it also includes reptiles, birds and arthropods. On several occasions occupied and unoccupied roosts of the barn owl were found deep in the dune area on dune slopes under S. sabulicolata plants. Owls can therefore be expected to be active throughout the dune area, and not only within reach of river-beds and mountains.

5.3 Small predators

These include the golden mole Eremitalpa granti namibensis (No. 4), three geckos (Nos. 10 – 12), three lizards (Nos. 9, 13, 14), the chameleon (No. 15), the desert chat (No. 16) and a number of insectivorous birds which may occasionally enter the area. Few of the species are strictly predatory, and the two omnivorous gerbil species (No. 3) are also discussed under this heading.

The Namib golden mole (No. 4) is a voracious insectivore which mainly inhabits the overgrown inland dunes, but whose distribution extends as far west as does the distribution of the dune grasses. It mainly feeds on root pseudococcids (No. 62) off the roots of dune grasses, but even took medium sized Palmatogecko (No. 12) in captivity. The biology of the species was recorded in some detail by Holm (1969). One specimen was trapped in 1969, and the nocturnal activity of the species is limited to the dunes and was recorded throughout the year (Fig. 2).

Two species of barking geckos were found in the study area. Both are nocturnal, but also emerge on cold overcast days. Ptenopus garrulus (No. 10) is a widespread species, but is restricted to the plains in the study area (Fig. 3). Members of the genus are all fossorial, and make characteristic territorial barking noises at their tunnel entrances (see Brain 1962; Haacke 1969, 1974, 1975, 1976a – c). Stomach contents of two specimens taken on 26.11.1969 (both with inactive gonads) corroborated earlier observations that these geckos mainly feed on social insects.
The second species of barking gecko, *P. kochi* (No. 11) has a more restricted distribution and is probably restricted to the central dune area. It is, as is the case with the previous species, never found on higher dune slopes or the dune crest. The contents of four stomachs taken on two different dates clearly show the opportunistic feeding pattern which is characteristic of desert animals. It is interesting to note that vegetable matter occurs in the diet, as in the case of *Aporosaura* (No. 13):

<table>
<thead>
<tr>
<th>Prey sp.</th>
<th>1♂</th>
<th>1♀</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. 58</td>
<td>13</td>
<td>8</td>
<td>21</td>
</tr>
<tr>
<td>No. 68</td>
<td>3</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>No. 69</td>
<td>4</td>
<td>4</td>
<td>8</td>
</tr>
</tbody>
</table>

The geographical range of *P. kochi* is strictly nocturnal, and tunnels in the dune slopes but also hunts in the dune crest and plains areas (Fig. 4). The species occurs in all dune areas of the Namib, as is the case with *Aporosaura* (No. 13) and *Batis peringueyi* (No. 7). The extraordinary webbed toes of this gecko enable it to walk rapidly on soft sand, and to dig tunnels in the soft sand of the dune slopes very effectively. The animal is very weakly pigmented and appears translucent. It uses its tongue to wipe dust off the large and exposed eyes. *Palmetogekko* is the most abundant nocturnal reptile in the dunes, and seems to be more active in summer (Fig. 2). It is heavily preyed upon by various vertebrates and possibly even sparassid-spiders (Lawrence 1959), and in turn seems to feed on all nocturnal dune arthropods of manageable size, as reflected in stomach contents:

<table>
<thead>
<tr>
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</thead>
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<td>46</td>
</tr>
<tr>
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<td>59</td>
<td>67</td>
<td>—</td>
<td>—</td>
<td>126</td>
</tr>
<tr>
<td>No. 62</td>
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<td>—</td>
<td>—</td>
<td>37</td>
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<tr>
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<td>—</td>
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</tr>
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</tr>
<tr>
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<td>—</td>
<td>3</td>
<td>—</td>
<td>3</td>
</tr>
<tr>
<td>grass seeds</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>7</td>
</tr>
<tr>
<td>grass leaves</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>7</td>
</tr>
</tbody>
</table>

*Palmetogekko rangei* (No. 12) is strictly nocturnal, and tunnels in the dune slopes but also hunts in the dune crest and plains areas (Fig. 4). The species occurs in all dune areas of the Namib, as is the case with *Aporosaura* (No. 13) and *Batis peringueyi* (No. 7). The extraordinary webbed toes of this gecko enable it to walk rapidly on soft sand, and to dig tunnels in the soft sand of the dune slopes very effectively. The animal is very weakly pigmented and appears translucent. It uses its tongue to wipe dust off the large and exposed eyes. *Palmetogekko* is the most abundant nocturnal reptile in the dunes, and seems to be more active in summer (Fig. 2). It is heavily preyed upon by various vertebrates and possibly even sparassid-spiders (Lawrence 1959), and in turn seems to feed on all nocturnal dune arthropods of manageable size, as reflected in stomach contents:

<table>
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<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>No. 68</td>
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<td>—</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Unidentified salticid</td>
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<td>—</td>
<td>—</td>
<td>1</td>
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<td>—</td>
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<td>2</td>
</tr>
</tbody>
</table>

An extensive analysis of the diet of this species was given by Robinson & Cunningham (1978).

*Aporosaura anchietae* (No. 13) is a fast moving diurnal lizard of the dune crest system (Fig. 4), with territories and harems on the dune slip-faces where they mainly hunt for small arthropods and grass seeds in the detritus. The biology, physiology and behaviour of this animal have been the subject of a number of studies (Louw 1972; Louw & Holm 1972; Holm 1973; Robinson 1977; Robinson & Cunningham 1978). Juveniles have bright yellow tails, adults are cryptically coloured. Specimens were trapped regularly throughout 1969 except in a two month spell between April and May (Fig. 2). The diet activity is distinctly bimodal in summer and unimodal in winter (Fig. 3), and the underlying circadian rhythms for these patterns were investigated by Holm (1973). Stomach content analyses are given in Louw & Holm (1972) and much more extensively by Robinson & Cunningham (1978), and are not repeated here.

*Chamaeleo namaquensis* (No. 15) was only seen once in the study area, but is relatively common in the overgrown inland dune area. It can manage even the largest and hardest dune tenebriions. The biology and ecology were discussed by Burrage (1973).

*Typhosaurus brauni* (No. 9) is the most elongated legless lizard known. It is active throughout the year (Fig. 2), mostly among *S. sulliculca* hummocks in the dunes (Fig. 4). It presumably lives on the dune termites (No. 59) and the thysanuran which are particularly abundant in its habitat. Like the mole (No. 4) it has a
habit of moving either on the surface or just submerged, and leaves very characteristic tracks. The species seems to be abundant wherever dune grasses grow. The nose is sharply pointed, and the lizard can swim into (even relatively compacted) sand at an amazing speed.

*Gerbillurus paeba* (No. 3), the pygmy gerbil, is commonly found in the area south of Gobabeb, where it mostly constructs its burrow under narra plants (Fig. 4). This species roams over all habitats at night, feeding on arthropods and seeds, chiefly on those of the narra. It is apparently heavily preyed upon by owls and jackals (see above). Activity is seemingly constant throughout the year (Fig. 2). Another species, *G. valinias*, was recorded in the study area on occasion, but seems to prefer the Kuiseb river-banks (see also Laycock, 1975).

The only insectivorous bird which resides more or less permanently in the area is the desert chat (No. 16), and a nest was found on a small rock in the study area. This species was mostly seen hunting on the plains, often feeding on ants at the ants’ nest entrances. After rains a variety of insectivorous birds (and even birds which are normally not insectivorous like geese and herons) converge on the area and feed on the abundant arthropods.

The general fauna and ecology of the area have been discussed in many of the specialised papers on the Namib Desert, and in some papers devoted entirely to this purpose (Lawrence 1959; Koch 1961; Robinson & Sealy, in prep.), while a number of papers have appeared which deal with groups of the vertebrate fauna (e.g. mammals: Coetzee 1969; reptiles: Mertens 1972; Haacke 1975, 1977; birds: Willoughby 1969, 1971; Prozesky 1969; Dixon 1973).

### 6 CONSUMERS: INVERTEBRATES

A study on micro-organisms (le Roux 1970) revealed low levels of microbes in the sand, and even in the detritus of the dunes at Gobabeb, with the highest counts (in most groups) in the interdune plains and lowest counts in dune slope sands. Few nitrifying bacteria were present in dune sand and none in the interdune, while levels of cellulose degrading fungi were low even in sand with detritus.

Nothing is known of non-arthropod invertebrate animals in the dunes.

The arthropods, on the other hand, are the most important consumers in the system in terms of diversity, energy turnover and key functions, and the community in the dunes at Gobabeb is taxonomically, physiologically and behaviourally one of the best studied in southern Africa.

At order level the composition of the arthropod groups seems normal (although the relatively small community of only about 120 species makes such a statement rather meaningless). Coleoptera account for roughly one-third of the species, and Hymenoptera and Diptera occur in about the normal proportion of approximately 5 – 10% each. Lepidoptera (not recorded in this study) are apparently scarce with only a few known highly adapted species, while spiders, solpugids and thysanurans are exceptionally well represented. Within the orders and families the distribution of groups becomes progressively more uneven. Thus 70% of all beetle species are tenebrionids, of which 70% in turn are represented by the tribes Adesmiini, Zophosini and Eurychorini. Similar one-sided representations are found within the scarababids, weevils, spiders and solpugids. At family level the species distribution becomes extremely uneven (see e.g. Onymacris, Leptidochora, Vernayella and Leptostethus against the many genera with only one representative). This progressive unevenness down the taxonomical hierarchy combined with the high endemism within the well-represented groups (see below) lends itself to interesting speculation on the evolution of the fauna which, however, goes beyond the scope of this study.

When numerical dominance is considered (as roughly reflected in Fig. 2) the beetles, and more specifically the tenebrionids, are responsible for the major proportion of the fauna and are probably responsible for most of the energy turnover as they are low in the trophic chains, small and extremely active.

Two-thirds of the recorded arthropod species are apterous, and few of the alate species are endemic or specially adapted to the system. This high incidence of alary is partly due to the success of apterous groups (e.g. the tenebrionids, spiders, solpugids and thysanurans) and partly due to endemic alary (e.g. among the scarabaeids). The most obvious reason for alary is the coastal position of the desert and the high incidence of seaward storms, but a number of other factors may contribute. Fossorial life (and in some habitats sand-diving) is essential in most niches, and does not

FIGURE 2: Daily macroclimatic and total daily trapings of nine pit traps for four months of 1968 and eleven months of 1969. Numbers above species names are code numbers (see p. 34–36); numbers behind histograms are totals of specimens trapped. For 1968 only weekly averages of the dominant Tenebrionidae are given, and traps were only operated every second week. For 1969 all daily trapings are recorded, with the dominant Tenebrionidae on % scale. Circles are sightings or records of fresh tracks. For the periods 25.II – 1.III; 3.III – 8.III; 22.III – 2.IV; 22.VII – 24.VII and 24.VII – 27.VII averages are given, but where these are below one, totals are recorded on the first days of the period. For No. 69 only the occurrence of alates (vertical arrows, also on No. 70) is recorded, since these ants could climb out of the traps. Histograms are not corrected for missed trapping days on individual traps (see text).
<table>
<thead>
<tr>
<th>Month</th>
<th>Species</th>
<th>Abundance</th>
</tr>
</thead>
<tbody>
<tr>
<td>FEB</td>
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<td>1105</td>
</tr>
<tr>
<td>MAR</td>
<td>Vernayella delabelli</td>
<td>21</td>
</tr>
<tr>
<td>APR</td>
<td>Vespheodes</td>
<td>10</td>
</tr>
<tr>
<td>MAY</td>
<td>V. noxigera</td>
<td>11</td>
</tr>
<tr>
<td>JUN</td>
<td>V. paulinii</td>
<td>112</td>
</tr>
<tr>
<td>JUL</td>
<td>Calamagrostis phalaroides</td>
<td>78</td>
</tr>
<tr>
<td>AUG</td>
<td>Stipa stellata</td>
<td>18</td>
</tr>
<tr>
<td>SEP</td>
<td>Lepidochora portulaca</td>
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</tr>
<tr>
<td>OCT</td>
<td>L. leucophaea</td>
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</tr>
<tr>
<td>NOV</td>
<td>L. discoides</td>
<td>1262</td>
</tr>
<tr>
<td>DEC</td>
<td>Pachystemobus albomaxatus</td>
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<tr>
<td></td>
<td>P. castanea</td>
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<td></td>
<td>Plateaulea ecosia</td>
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</tr>
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<td>C. carinatae</td>
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<td>C. cornuta</td>
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<tr>
<td></td>
<td>Zaphlora orbiculata</td>
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</tr>
<tr>
<td></td>
<td>Litoria moralesii</td>
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<td>C. argentea</td>
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<td></td>
<td>O. albo-septata</td>
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<td></td>
<td>O. albiloculata</td>
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<td></td>
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<td></td>
<td>Phasmaphalax melanoptera</td>
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</table>

**FIG. 2 (cont.)**
FIGURE 3: Average daily cycles of macroclimate for summer and winter months, with totalled trappings of four timed pit traps. Curves on histograms are hand-fitted for easier reading. Missed or partially missed trapping days on individual traps are omitted from the data.
FIGURE 4: Diagrammatic cross-section through the study area with positions and photographs of the nine trapping stations (plan in Fig. 1), and percentages of the various species trapped in each. Code numbers precede species names, specimens are recorded for every column and are followed by totals. Columns 1 to 9 correspond with trapping stations 1 to 9. Histograms are crudely corrected for missed trapping days, and are not evaluated statistically (see text).
combine well with alateness (none of the sand-diving species is alate). The spatial distribution of detritus deposits, and their persistent nature, probably reduces the need to fly in detritivores, which might add to the high incidence of apterousness in this trophic category, very markedly expressed in the family Tenebrionidae, which is also predominantly apterous in other ecosystems such as e.g. the Kalahari and the savanna systems in Africa.

It is difficult to assign food niches to the various taxa, since virtually all desert animals are more or less euripagous opportunists. The trophic web given in Fig. 5 must therefore be seen as a rather crude generalisation. For convenience, we shall discuss the arthropods under their predominant functions as primary feeders, detritivores, coprophages and predators.

6.1 Primary feeders

Virtually all primary feeders among the arthropods in the system are dependent on rain and only emerge after rain. Emergence is timed to coincide with the growth stage of the host plant which is then attacked (see Fig. 2). Primary feeders on the perennials include most of the species with wide distribution elsewhere, and with a few exceptions these too were only recorded in the study area after rains. A number of detritivores and omnivores also utilise the green growth after rain, with spectacular increases in their populations, mostly due to influx from surrounding areas and increased activity, sometimes combined with real population build-up (see Nos. 47, 106, 135, 136 in Fig. 2). A few primary feeders are little or only indirectly affected by rain. These include the focrilous flies and wasps (Nos. 85 – 86, 77 – 80), the narracricket (No. 52) and the pseudococcid (No. 62). Most of these, including the unidentified and presumably sap-sucking Heteroptera (Nos. 63 – 65) and the buprestid and meloid species (Nos. 94 – 96) were rare in the study area.

Nos. 53 – 57: Grasshoppers and locusts. Apart from No. 53 which is endemic and apterous, all these orthopterans are widespread alate species which occur after rain and feed on the annual grasses. Crypticerus cubicus (No. 53) is the dominant species and well adapted to the desert conditions. It is cryptically coloured with short antennae which fit into grooves on the head (Brown 1962), and has hindlegs which are bright red on the inside. The species is found on the lower dune slopes and plains where the annual grasses grow after rain (Fig. 4). The first peak in population activity (Fig. 2) was early in April and only first instar nymphs were recorded. Later all stages occurred, and at the end of June much predation by birds and arthropod predators was evident, whereafter the population rapidly declined and disappeared.
FIG. 6

FIGURE 6: Beetles recorded during the 1969 trapping survey in the dunes south of Gobabeb. Numbers relate to the check-list on p. 34–36.
FIGURE 7: Some of the more common non-coleopterous arthropods recorded during the 1969 trapping survey in the dunes south of Gobalheb. Numbers relate to the check-list on p. 34–36.
Nos. 58 — 59: Termites. Whilst No. 59 may be found in the dunes long after rains, No. 58 only seems to maintain colonies permanently in areas with fairly regular rains (see Coaton & Sheasby 1973). Both species were recorded in the dune area in 1969, with No. 58 mainly in the plains and No. 59 higher on the slopes and in dune valleys (Fig. 4). Both species produced alates in February and March 1969 after the rains. Both species may equally well be classed as detritivores, since they also collect dry grass.

No. 60: The dictyopharid species. This small cryptically coloured species was first recorded in this trapping survey, and has as yet not been named. It occurs on the dune slopes and dune foot in winter, and might be rain dependant as the members of the family are sap-suckers. It is a diurnal species, a very good jumper and is brachypterous.

Nos. 98 — 103: The weevils. All the weevil species are only active as adults after rain. No. 98 is a small green species which is only found in the plains and dune foot area (Fig. 4). It was predominant in stomach contents of Aporosaura (Louw & Holm 1973) but since few were trapped (Fig. 2) the species was presumed to move around very little. No. 99 occurs exclusively under Triantloma shrubs (Fig. 4), and is rarely seen on the surface, except after rain (Fig. 2). No. 100 occurs mainly on the dune slopes but also in the plains, wherever the lily, which it feeds on, grows. While it is certain that B. rotundatus is the common Brachicerus species in the area, there may be other species associated with less abundant lily species since most flies are attacked by Brachicerus spp. The curculionid fauna on the short-lived annual vegetation in the Namib has not been surveyed systematically, and may prove a most rewarding field for taxonomists. Nos. 101 — 103 all belong to the genus Leptostethus, and these three species show a curious trimodal diet activity (Fig. 3) which may not be significant for Nos. 101 and 103, but for No. 102 is well demonstrated. This modality is not understood. All three species occur on the dune slopes and No. 103 also wanders over the crest area resulting in high catches in trap 4 due to the channelling effect of the slip-face basking (Fig. 4). The delay in emergence after rain is proportional to size differences, whilst the population lifespan is inversely proportional to body size and population size (Fig. 2). All the Leptostethus spp. show thanatosis as a reaction to disturbance. They lay their eggs at the base of plants after digging a crater in the sand with their hind legs. No. 101 is a hardy species, and individuals found early in 1969 were survivors of the population which emerged after the rain late in 1968. It is euryphagous, feeding on the annuals but also on Triantloma, S. sabulicola and even A. horrida. No. 102 is a beautiful large blue weevil, and not yet described. It only feeds on green S. sabulicola leaves after rains, and populations are then very large but short-lived (Fig. 2). In the period 1964 to 1969, the species only occurred in the exceptionally rainy years of 1967 and 1969. In spite of heavy predation on these relatively soft-shelled and slow-moving animals by birds and arthropods, the population was not overtaken by the predators, and dead but intact specimens littered the dunes at the end of July. No. 103 is similar to 102 in habits, but is not as abundant (Fig. 2). It feeds on Triantloma exclusively (Fig. 4).

Nos. 124 — 125: The Pachynotus spp. The two most common species of this genus in the study area are P. albomaculatus (No. 124) and a species which we provisionally hold to be P. mackadai (described from the northern Namib). Two other species have been recorded near Gobabeb. No. 125 is the smaller and more common species (Fig. 2), and feeds on the grasses in the plains (Fig. 4). No. 124 is rare and individuals survive for shorter periods after rains (Fig. 2). They feed mainly on S. sabulicola and are therefore mostly trapped on the dunes (Fig. 4). Both species are very clearly rain-dependent, and completely absent in dry years such as 1968. At least No. 124 seems to have a moisture-terminated quiescence, since a small population emerged in September after very little rain in August (Fig. 2). Both species have well-developed bristles on the legs, which they use to dig themselves in at night, and to dig craters for egg-laying at the stems of grasses. Activity is diurnal.

No. 130: Euystolopus octosertatus. This is the only member of the tribe Adesmiini in the system which is a true rain-dependent form. Its occurrence coincides with that of No. 125 (Fig. 2), and feeding habits are also similar. It is a small species (Fig. 4) and tunnels into the sand at night. Single individuals may be found out of season, but after rains the species becomes extremely abundant. In 1967 an estimated density of one specimen per metre square was reached in the plains, and over 3 000 specimens were trapped in a pit trap in three days. The fact that comparable densities were not reached after much better rains in 1969, suggests that a prolonged quiescence may be possible, which could result in a large synchronised crop of individuals after an extended drought period such as preceded 1967.

The alate primary feeders were not well covered by this survey. Several species of Lepidoptera occur on both the perennial and annual vegetation (Wharton, pers. comm.) and at least one aphid species is present. The presence and diversity of other alate groups, such as the Heteroptera, may also be significantly greater than reflected in our list.

6.2 Detritivores and omnivores

The detritus feeders are the largest group in the system in terms of individuals and are second only to the predators in number of species. The abundance and ecological importance of the detritivores in the Namib Desert dune ecosystem has been pointed out by Koch (1961) and others (e.g. Lawrence 1959, Seely 1978c). The distribution of the abundant detritus to various habitats was described under "wind" above, and the
variety of habitats combined with the heterogeneity of the detritus itself, offers a wide variety of niches to detritivores. The detritus consists of grass seeds, grass blades and stalks, dead arthropods and other animal and vegetable matter. Particle size varies from whole grass clumps to organic dust. Little is known about the feeding preferences of the various detritivore species, but it may be assumed that the energy- and protein-rich parts will be preferred by most species (within their capability of physically ingesting them), and that the quality of a given sample of detritus would decline with feeding much more rapidly than the quantity. Thus the large accumulations of detritus on dune slips may not signify an abundance of food for all detritivores, and the advantages of exploiting new supplies first may be great. This may explain why the most successful species on the dune crest (e.g. Nos. 110 and 117) are those which are able to withstand the desiccation of eastern storms (which carry the highest load of fresh detritus).

The most important groups in this feeding category are the tenebrionids, with about thirty species and the thysanurans with four. The detritus ant (No. 69) probably contributes substantially to detritus removal, since it is one of the numerically dominant species, but is also predatory on small arthropods. A number of species alternate opportunistically between primary feeding and detritus feeding (see 'primary feeders' above) and few detritivores are not attracted to arthropod or other animal carcasses in their habitat (rotten meat is an excellent bait for virtually all detritivores of the dune crest). Some of the detritivores in our discussion are classified as such by inference rather than observation and in a few cases (e.g. 121, 126, 128) this designation of trophic niche is no more than a guess.

Once detritus becomes submerged in sand, it is even more difficult to establish its fate. In shallowly submerged deposits there are usually some tenebrionid larvae and many thysanurans, and also some of the smaller tenebrionids. It is, however, not known whether all tenebrionid larvae feed on detritus only, since the roots of the perennial plants and even the annuals offer an alternative source of underground food.

Nos. 47 - 50: The thysanurans. These animals, like the tenebrionids and arachnids, are well pre-adapted to desert life by way of their diet, their ability to crawl into small hideouts and their drought resistance. It is likely that myrmecophilous and termitophilous species of thysanurans occur in the area apart from the four free-living species we recorded. No. 49 is the largest, and has black and ochre bands. Its activity is mainly nocturnal-crepuscular (Fig. 3), and it occurs all over the area (Fig. 4) throughout the year (Fig. 2), but was not recorded in February and March, suggesting that the population only became established after the rains. This species either tunnels or sand-dives, and otherwise has the habit of lying in a shallow depression in the sand with the exceptionally long antennae and cerci stretched out on the surface. No. 47 is the most common species and occurs mainly in the sand hummocks under perennials (Fig. 4). Activity is distinctly bimodal in summer and winter, with peaks after sunrise and around sunset (Fig. 3). Activity increased significantly after rain and during spells of east wind (Fig. 2). No. 48 is strictly a plains dweller (Fig. 4) and is a very smooth light silvery grey species. It is present but not common throughout the year (Fig. 2) and is nocturnal. No. 50 is the most specialised species of the group and occurs in the dune crest area (Fig. 4). A distinct diel activity pattern was not recorded (Fig. 3), because the species becomes active during strong winds at any time of the cycle. The yearly trapping data show a near perfect correlation between east wind occurrences and activity of the species (Fig. 2). This as yet undescribed species is cryptically coloured, very robust, virtually naked and has short transformed cerci. It is a very competent sand-diver and was never found far from the slips. Edney (1971a) and Holm & Edney (1973) have reported on behaviour and physiology of some of these thysanuran species.

Nos. 104 - 109: Small nocturnal tenebrionids. It is noteworthy that all these closely related species of below 3 - 4 mm in length are nocturnal. Diurnal activity for this size range of apertural ground-dwellers is probably restricted by the poor volume to surface area ratio and consequent vulnerability to overheating and dessication. The six species all occur on dune sand exclusively, and are sand-diving. They all seem to occur throughout the year, but the activity of No. 106 increased following the rains, and was markedly higher in winter. Habitat niches overlap, with all the Vernayella species occurring on the dune crest, with only slight differences in activity on the crest slip-face or slip-face base between the species (Fig. 4). No. 108 is clearly a dune slope species concentrating around Trianthema, while No. 109 also seems to occur in the sandier parts of the plains (Fig. 4). We only had the opportunity to observe Nos. 106 and 107 feeding on small detritus particles, but it is not unreasonable to assume that this is what all these species feed on. No. 104, which is the palest and smallest of the species, is more often found in detritus pockets than on the sand surface.

No. 109, which belongs to the tribe Zophosini, is a globose species with extreme morphological adaptations to a submerged way of life, and it probably rarely surfaces. It was previously believed to be blind, but has well hidden and protected eyes (Penrith 1974 and pers. comm.). This group of small tenebrionids showed the greatest degree of niche overlap between species in this study, and would probably need a more refined and intensive approach to be understood.

No. 122: Psammogaster malani. This small species is quite unrelated to the above. It is a sluggish crepuscular animal, often found in submerged detritus. It occurs throughout the year (Fig. 2), mostly near the dune crest but also on sandy spots throughout the area (Fig. 4).
It is a very widely adapted species with wide distribution in the dune areas.

Nos. 110 — 114: Small diurnal tenebrionids. All members of this group belong to the Zophosini, which is a very widespread and successful diurnal group in Africa and which is also extremely successful in the Namib Desert (Koch 1962, 1969; Schulze 1974; Penrith 1977). No. 110 is a small species with yellow markings and which normally occurs on the dune crest (Fig. 4) but is sometimes found to traverse dune slopes from one slip-face to the other. Activity is strictly diurnal (Fig. 3) throughout the year but more prominent in winter (Fig. 2). They are very efficient sand-divers and are active during storms, when they are carried by wind eddies on the slip-face to land with the detritus. The fast and erratic movements combined with the yellow colour make these insects hard to see in whirling sand and detritus. They are attracted in great numbers to carcasses of reptiles or gerbils near the slip-face. Hamilton (1971) reported on the biology of the species. No. 111 is a smaller congenor of No. 110 which was only recently discovered due to its small size and cryptic colouration (Koch 1969). It occurs throughout the year (Fig. 2) but from visual observations in 1968 and 1969, is more abundant in March and April. The species is restricted to the dune foot (Fig. 4) where it uses the detritus to create a micro-dune (see 'substrate' above). Activity is diurnal (Fig. 3). No. 112 is a very fast runner, with a bluish wax secretion on the black integument. It is the most numerous species in the system and is strictly a winter form with population activity peaks coinciding with spells of east wind (Fig. 2). It occurs on the dune slopes and dune foot, between the areas of activity of No. 110 on the one side and Nos. 131 and 113 on the other (Fig. 4). Activity is clearly bimodal (Fig. 3). No. 113 is a bit slower and more compactly built than the previous species. It is one of few species in the system with a pronounced summer activity, although it occurs throughout the year (Fig. 2). It occurs on the plains and dune foot (Fig. 4), and the diurnal activity is clearly bimodal with emphasis on afternoon activity (Fig. 3). Stomach contents of this species revealed small seeds and fragments of grasses, but specimens were seen to feed on thysanurans on two occasions where it is not certain whether they killed them or found them dead. After the rains, feeding on green grass was repeatedly observed. At night the beetles sleep under tufts of grass or pebbles, often half exposed, and they do not dive into the sand. Of 400 specimens which were marked on three different occasions, trap retrieval of marked individuals in each instance decreased sharply after about ten days, and we suspect the adults to be short-lived in contrast to the larger tenebrionids in the area. No. 114 is very similar in appearance and habits to No. 113, and is more common in the river-bed. In the study area it occurred throughout the year (Fig. 2) and in all habitats, but most specimens were trapped at the slip-face base (Fig. 4). It is also a diurnal species and fairly widespread, but as it is restricted to the dunes close to river-beds and mountains it may be regarded as a marginal species in the study area.

No. 131: Cauricara platangum. Ecologically this species belongs to the previous group, since it is a fast and small diurnal tenebrionid. It belongs to a different tribe, however, and has a very different morphology and behaviour from the species above. The extremely long legs of the species enable it to achieve high speed on the plains, and also serve to lift the body away from the hot sand surface (Henwood 1975a) and thus to enable it to be active throughout the noon period (Fig. 3). It is strictly a plains dweller (Fig. 4) and is winter active (Fig. 2). The slender build of these beetles is a disadvantage under windy conditions, and unlike the other detritivores, it is most active between spells of east wind (Fig. 2). Sand-diving is also impossible for this species, and at night they attach themselves to grass clumps and pebbles, where they are preyed upon by spiders, solpugids and scorpions, which usually leave the thorax, head and legs of the beetles still firmly attached to the grass stems. The trophic, habitat and diel activity niches of this species overlap with those of No. 113, and the population of the latter decline when C. platangum becomes active. Food is, however, much more plentiful in winter, which makes it possible for Z. moralesi to maintain a population in spite of much niche overlap with C. platangum.

Nos. 115 — 118: The Eurychorini. These are all nocturnal species of medium size and with more or less circular and flat bodies, probably originally evolved for living under bark and rock, and further adapted to sand-diving by the loss of sculpture and the addition of scales in the genus Lepidochora. The Lepidochora species are heavily preyed upon by Palmatogecko and spiders, and instances of predation by both were often seen. No. 115 is the largest of the species occurring at Goebabeb. It occurs throughout the year (Fig. 2), is strictly nocturnal, and it is restricted to the dune crest area (Fig. 4). No. 116 is smaller than the previous species, and not as flat. It occurs on the dune slopes (Fig. 4) and is more active in summer (Fig. 2). The activity is strictly nocturnal and decreases with decrease in temperature, with a resultant marked shift to the early night hours in winter (Fig. 3). Both No. 115 and 116 are able to withstand low temperatures, and were found on the surface at ambient temperatures of below 5°C. No. 117 is much more abundant and active than the previous two species, and clearly more so in winter and after rain (Fig. 2). Activity is very closely correlated with wind, as in the case of other dune crest detritivores. This species only leaves the slip-face when it migrates to another (Fig. 4). Since we had no timed trap on the slip-face, the diel activity in Fig. 3 is based on traps outside the normal microhabitat of the species. It consequently reflects these odd migrations and is therefore rather misleading. On the slip-faces activity is crepuscular-nocturnal, but the animals come out and forage en masse during the
throughout the year, but is more abundant in summer.
Nos. 119, 120 and 121 are dune-edge species which
occur along all the river-beds and washes in the insel-
bergs, in relatively loose sand near vegetation. They
are all nocturnal and individuals may occasionally be
found in the dunes. It is difficult to decide to what
extent these odd intruders into the dune system form
part of the ecological community. Other tenebriionids
like Eurychora spp. and Epiphylla spp. may also
enter the marginal dunes in some areas and may even
maintain populations there on a limited scale. Apart
from the references cited under groups and species
of tenebriionids above, a number of studies have dealt with
the tenebriionid fauna at Gobabeb in general, or with
aspects pertaining to several groups. Apart from the
pioneering work by Koch (1961, 1962a, b) studies by
Edney (1971b), Hamilton (1973, 1975), Holm & Edney
(1973), Lawrence (1959) and Seely (1973) were also
undertaken.

Finally under detritivores we must mention the ants
(Nos. 69, 70) and termites (Nos. 58, 59). Of these
only No. 69 is permanently active in the system at
Gobabeb; the other species enter after rain, and gradu-
ally disappear in dry years (see No. 70 on Fig. 2).
These species have been discussed elsewhere, and their
relative population activities and contribution to detritus
removal could not be established by our methods.
The detritus ant (No. 69) is not only detritivorous,
but also tends the aphids and No. 62 for honeydew,
and furthermore preys on small arthropods. Nests seem
to be territorial, since a full scale "war" between two
colonies was witnessed on a bare dune slope by
W. J. Hamilton (pers. comm.).

6.3 Predators and parasitoids

The diversity of arachnid predators in the dunes is
extremely high compared with that of primary feeders
and detritivores, especially considering their position
above the second trophic level. The fourteen spider
especies, eight solpugids and two scorpions which were
recorded are probably not a complete list for the area;
many were only collected once or twice, and the chances
that other species were not recorded at all are good.

The largest spiders may be able to prey on small geckos
(Lawrence 1959), and spiders and solpugids were
repeatedly seen to feed on tenebriionids (Lepidochora,
Zophostis, Ceroptis and Caucicara species). Smaller
species probably feed on thysanurans and ants. Predation
also occurs within and between the arachnid
groups.

Trapping results of all but two species were low, and a
full ecological analysis is therefore precluded. The
biology of most of the species has been commented
on by Lawrence (see references below), and an
ecological survey of the group is presently underway
at Gobabeb (Whaton, pers. comm.). We therefore
only provide a few notes of our own which do not on
their own do justice to this group (which is evolu-
tionarily, behaviourally and ecologically at least as
interesting as the tenebriionids in the Namib dunes).

Nos. 29 – 42: The spiders. While trapping results of
all spiders were low (Fig. 2), some of the species’
habitat preferences can be read from Fig. 4. The
salticids (Nos. 39 – 41), palpimanids (Nos. 33, 38)
and thomids (No. 35) are invariably found in or near
plants, while the large nocturnal paraspidids (Nos. 30,
31, 34) hunt over the whole area. No. 30 is often
found on the dune crest, and has the unique behaviour
of “cartwheeling” down the slip-face to evade enemies.
All paraspidids dig tunnels in the firm dune slopes
in which they shelter in daytime. One of the most
extremely adapted spiders is No. 29, which lives in the
loose sand of the slip-face near the crest. It is a small,
very robust species with short hairy legs, and can bury
itself very rapidly in the soft slip-face by lying on its
back and working the sand around it upwards with the
legs.

Nos. 21 – 28: The solpugids. The three diurnal species
(Nos. 21 – 23) were trapped in much larger numbers
than the remaining five nocturnal species and are all
more abundant in summer (Fig. 2). No. 21 occurs all
over the area (Fig. 4) and is highly thermophilic, being
most active at noon, both in summer and winter (Fig.
3). No. 22 is similar in size, prefers the dune slopes
(Fig. 4) and has a bimodal-diurnal activity cycle in
summer and winter (Fig. 3). The latter species is
reddish like the dune sand, and hunts on the ground
as well as up the stems of S. sabulicola plants.
Nos. 23 and 25 are clearly restricted to the plains,
with the former diurnal and the latter nocturnal. No.
25 is very robust and buries itself in the sand as does
spider No. 29.

Nos. 43 – 45: The scorpions. Very few of these were
trapped, but habitat preferences could be determined
from burrows. No. 43 tunnels in sandy spots in the
interdune plain. No. 44 under plants near the dune foot
and No. 45 is petrophilous.

No. 46: The velvet mite. These bright red predatory
mites occurred after rains in the dunes and the
population persisted for about three months (Fig. 2)
on the lower dune slopes and interdune plains (Fig.
4).

The arachnid fauna of the Namib Desert has been
studied extensively by R. F. Lawrence (1959, 1962a,
b. 1965a, b. 1967, 1969, 1972) and subsequently by
Lamoral (1972) and Newland (1972).

Predators amongst the insects are, with a few excep-
tions, alate and wide-spread species. The two tettigo-
nids (No. 51 and 52) are at least partially predatory.
No. 51 is strictly nocturnal and occurs throughout the
year (Fig. 2) mainly on the dune slopes (Fig. 4). This
species, like some of the thysanurans, is often found
in a shallow depression on the slopes, with the extremely
long antennae stretched out on the sand surface.
Whether or not this is an ambush posture could not
be established. No. 52 was only found near narra
bushes (Fig. 4) or traversing dune slopes from one of these to the other. Of the predacious hemipterans, only No. 61 was trapped in significant numbers. This species occurs throughout the year (Fig. 2) mainly under *Trianthema* (Fig. 4). The neuropterans of the Namib have not been studied systematically, and it is possible that more than two species (No. 66, 67) occur in the dunes at Gobabeb. Both species were rarely seen (Fig. 4). The only mantid species (No. 68) was found in a *Trianthema* plant.

Of the large number of hymenopterans, only the dominant ones were recorded, and only the two apterous species were trapped in significant numbers (No. 71 and 72). Both occurred throughout the year (Fig. 2), with No. 71 on the dune slopes and the much smaller No. 72 mainly in the interdune plains (Fig. 4). The most common wasp in the dunes is No. 74 (Fig. 2), which tunnels in the dune slopes but hunts spiders, mainly sparrasids, in all habitats (Fig. 4). The parasitic No. 76 is as yet the only recorded encyrid species from the area, and was bred from No. 62 (Prinsloo & Annecke 1976).

A revision of the Miscophytes (Sphacidae) with very interesting data on the Namib fauna, is at present in preparation (Ole Lomholdt, in prep.). Through courtesy of the author we have had parts of the manuscript which deal extensively with matters of zoogeography and adaptation in this group, and contains many interesting notes, but we prefer not to forego the publication of these results here.

Amongst the flies, two asilid species (Nos. 82, 83) were regularly seen. Both occurred throughout the year (Fig. 2) and hunted mainly on the dune slopes (Fig. 4). No. 82 was seen to take *Cerasis* (No. 112) on several occasions. The flies of South Africa were revised recently by Lindner (1972, 1973, 1975), but no systematic survey of the dune-living forms has been done.

Three predacious beetles were recorded (Nos. 91, 93 and 97), and the larvae of the meloids (Nos. 94 and 95) are known to be predators, mostly on eggs of locusts and grasshoppers. No. 91 is a predator of aphids, which occur mainly on *S. sabulicola* grass. No. 97 is present throughout the year (Fig. 2) on dune sand (Fig. 4), and the histrids are known to feed mainly on maggots. No. 93 belongs to a tribe which is myrmecophilous, and this carabid is probably associated with the detritus ant (No. 69). Although it occurs throughout the year, a significant increase in activity was noted after the rains early in 1969 (Fig. 2). The beetles roam around hummocks of perennials on the dune slope (Fig. 4) at night. They are common throughout the central Namib dunes.

### 6.4 Coprophages and scavengers

While most detritivores will be attracted to carcasses to feed on them, a number of species are specialists in this food niche. Coprophages are few, and detritivores were never seen to feed on droppings.

The biology of the two wingless scarabs (*Pachysoma* spp. Nos. 87, 88) was recently described (Holm & Scholtz 1979, Holm & Kirsten 1979), and will be only briefly mentioned. No. 87 is a large species which occurs where oryx graze after rain, and forages exclusively on their dung. No. 88 is a small species which feeds on any droppings it can find, and also forages vegetable matter. This species is therefore intermediate between a coprophage and a detritivore. A small *Onthophagus* sp. was recorded on two occasions in the dunes, but is not included in the list since the records are most probably of stray specimens from the nearby Kuiseb river-bed. Both *Pachysoma* species are more abundant after rain (Fig. 2), and are strictly diurnal (Fig. 3). Their tunnels are excavated in the firmer parts of dune slopes (Fig. 4).

No. 84 is a small fly which may be found on the *Pachysoma* species as well as on No. 89, and these flies obviously use the scarabaeids to transport them to food. On several occasions the scarabaeids were seen entering their burrows with forage, and with flies on their back, to emerge without either. The advantages of apterousness in the Namib dunes are strikingly illustrated by this alate species being a transport-commensal of an apterous species.

No. 89 is a scavenger, and was only found to feed on carcasses. It has the same time and space niche as the *Pachysoma* species, and a similar distribution (see Holm & Kirsten, 1979). No. 92 is a well-known and cosmopolitan scavenger, but was rarely recorded in the study area since, unlike No. 89 which is attracted to dead lizards, snakes and gerbils, it only breeds in carcasses of large animals.

### 7 SPACE-TIME NICHEs

In a previous paper (Holm & Edney 1973) the diel activity patterns of some of the arthropods as illustrated by timed trappings were discussed. Experiments with *Aporosauro* (Holm 1973) support the theory that unimodal diurnal winter activity and bimodal diurnal summer activity are temperature induced strategies, at least in this species, and also clearly showed these patterns to be innate in this species. One possible reason for the differences between the rhythms of different species which Holm & Edney (1973) mentioned was the niche-exclusion principle, and when annual and spatial distributions are compared with diel activities, there seems to be more evidence for this, as examination of groups of closely related species may show:

Five *Onyvaris* species occur at Gobabeb, of which one (No. 135) is an opportunistic intruder in the area after rain, and not part of the normal niche pattern. The remaining four species occur throughout the year (Fig. 2). No. 132 is a coastal species which overlaps...
FIGURE 8: Maps of the central Namib with total blocks censused from 1975 to 1978, routes of the four expeditions and recorded distribution for 34 of the beetle species of the Gobabeb dunes. Stippling indicates dune ranges, black blocks are records from our survey and dotted blocks records from other collections (see acknowledgements). The latter blocks vary in accuracy, up to an error of 10'. Crosses are blocks in which we have reason to believe species do not normally occur.
Pan and Spencer Bay (northern limit of many species such as *Pachysoma bennigseni*, *Lepidochora pilosulae*, etc.) and one south of Walvis Bay (southern limit of e.g. *Cardiosis triangulifera*, *Lepidochora eberlanzi parva* etc.). These (probably historic) boundaries between species and communities cannot be interpreted only by the composition of the fauna that occurs at Gobabeb, and will be dealt with elsewhere.

Species Nos. 124, 125 and 131 are plains runners. They occur on plains near river-beds and rock outcrops, but also on interdune plains far removed from these. Their habitat preferences are not apparent at the resolution of the distribution maps, but can be seen in Fig. 4.

The species associated with river-beds and rocky terrain all enter the study area from the nearby Kuiseb river-bed (Fig. 1). Their distribution is chiefly sub-desertic, with extensions along river-beds and around inselberg formations. The present distribution and the differences in isolated populations of this fauna may shed more light on the history of migrations of dune barriers and climatic changes of the area (see e.g. No. 135), but an analysis of these phenomena would overstep the aims of this paper. Species which occur in this category are Nos. 113, 114, 119 — 121, 126, 129, 130, 134 and 135. As could be expected, this group contains most of the species which extend beyond the central Namib.

It is important to remember that distribution limits of the species are not constant, but extend and contract with temporary changes at the periphery of the species' distribution. Thus No. 132 was not recorded at Gobabeb before 1968, and has been constantly present since then. At present it seems to be disappearing from the area (Seely, pers. comm.). Similarly, No. 134 is present in some years and not in others, and Nos. 111 and 128 were only found at Gobabeb after several years of intensive collecting. Most boundaries of distribution in the dunes are unlikely to be maintained by competition, since (with the exception of some north—south barriers between coastal species) the areas of overlap between closely related species are generally wide (Fig. 8), and are more likely determined by niche preferences.

### 9 LIST OF ANIMALS RECORDED

<table>
<thead>
<tr>
<th>Code No.</th>
<th>Order</th>
<th>Family</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Artiodactyla</td>
<td>Bovidae</td>
<td><em>Oryx gazella</em> (L.)</td>
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<tr>
<td>2</td>
<td>Lagomorpha</td>
<td>Leporidae</td>
<td><em>Lepus capensis</em> L.</td>
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<tr>
<td>3</td>
<td>Rodentia</td>
<td>Cricetidae</td>
<td><em>Gerbillurus paeba Smith (+ G. vallinus</em> (Thomas))</td>
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<tr>
<td>4</td>
<td>Insectivora</td>
<td>Chrysocloridae</td>
<td><em>Eremita ipra granti namibensis</em> Bauer &amp; Niethammer</td>
</tr>
<tr>
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<td>c. (species with red carapace)</td>
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10 ACKNOWLEDGEMENTS

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GIESS, W.

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GOUDE, A. S.

GOUDE, A. S.

HAACKE, W. D.

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HAACKE, W. D.

HAMILTON, W. J. III

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HAMILTON, W. J. III, BUSKIRK, R. E. and BUSKIRK, W. H.
HAMILTON, W. J. III and SEELEY, M. K.

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HENWOOD, K.

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HERRE, H.

HOLM, E.

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LOGAN, R. F.

LOUW, G. N.

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NEL, J. A. J.

NEWLANDS, G.

PENRITH, M.-L.

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SEELY, M. K., DE VOS, M. P. and LOUW, G. N.

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SELBY, M. J.

STUART, C. T.

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WALTER, H.

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WILLOUGHBY, E. J.

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Prey selection by spotted hyaena (Crocuta crocuta) in the Namib Desert

by

Ronald Tilson
Desert Ecological Research Unit/Gobabeb
P. O. Box 1592,
Swakopmund, South West Africa

Frank von Blottnitz
Directorate of Nature Conservation,
Private Bag 13186,
Windhoek, South West Africa

and

Johannes Henschel
Desert Ecological Research Unit/Gobabeb,
P. O. Box 1592,
Swakopmund, South West Africa

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ABSTRACT

Species composition of prey eaten by three groups of spotted hyaena (Crocuta crocuta) in the central Namib Desert was evaluated. Age and sex categories of major prey are based on 55 carcasses and diets on 595 scats collected over 12 months. Gemsbok (Oryx gazella) was the most important food item in the overall diet of two groups, but in a third group gemsbok and mountain zebra (Equus zebra hartmannae) were almost equally represented. These differences were directly related to the availability of the prey within the hyaena foraging areas. Old animals of both prey species were the most common age class consumed by hyaenas. More male than female gemsbok were eaten, but female mountain zebra outnumbered males. Since hyaenas compete with no other large predator in the Namib, the composition of their diet reflects the sole impact of a predator/scavenger on a depauperate prey assemblage in a desert environment.
1 INTRODUCTION

The spotted hyaena (*Crocuta crocuta*) has dominated the early literature as a scavenger of carrion (see Kruuk, 1972), but recent studies have shown that part, and in some cases most, of the hyaena’s food is acquired by hunting (Eloff, 1964; Kruuk, 1970, 1972; Bearder, 1977; Mills, 1978). Except in the Ngorogoro Crater of East Africa, where spotted hyaenas are the dominant predator, kills made by lions (*Panthera leo*) or other large predators may contribute much to the diet of hyaenas, but the percentage can be difficult to assess (Kruuk, 1972; Bearder, 1977). This restricts any meaningful assessment of the impact hyaena predation may have on local populations of prey. It also affects the evaluation of prey selection because opportunistic scavenging from kills of other predators often cannot be distinguished from the results of individual or group hunting by hyaenas.

Here we report on the diets of three groups of spotted hyaenas that rest in sheltered areas along the Kuiseb River but forage out into the sand-dunes and gravel plains of the central Namib Desert. Gemsbok (*Oryx gazella*) and mountain zebra (*Equus zebra hartmannae*) are the two most abundant ungulates in this desert, and the spotted hyaena is their only predator. The absence of other large felids and canids distinguishes this area from any other African locality in which spotted hyaenas have been studied (Eloff, 1964; Kruuk, 1972; Bearder, 1977; see also Deane 1960, 1962; Hirsli, 1969; Pismaar, 1969; Mills, 1978). The absence of other predators enabled us to interpret the hyaenas’ overall diet and to evaluate their impact on the age and sex categories of the prey populations.

2 STUDY AREA AND METHODS

The research area, situated along the Kuiseb River in the Namib Desert of South West Africa, is about 75 km from east to west and 40 km wide. It includes about 3,080 km² from the Namib Research Institute at Gobabeb (23°34’S, 15°03’E) to the confluence of the Kuiseb-Gaub Rivers and parts of the northern gravel plains and southern sand-dunes (Fig. 1). It is an extremely arid area, receiving an annual rainfall of about 17 mm (1962–1972; Seely and Stuart, 1976). Most precipitation occurs in the summer months from January to March, although some rain may be recorded in any month with considerable variation from year to year (1962–1978 range = 0–125 mm, Gobabeb meteorological records).

The study area can be separated into three distinct habitats. South of the Kuiseb River lies the dune field of the Namib. Approximately parallel linear sand-dunes up to 100 m high are oriented in a roughly north–south direction and separated by interdune valleys about one kilometre wide. Trees and shrubs are absent, but there are scattered hummocks of *Trianthema hereroensis* on the dune slope and patches of grass (*Asipheratherum glaucum* and *Stipagrostis* spp.) in the sandy interdune areas. These plants are fed upon by several hundred widely dispersed gemsbok for all but the driest times of the year. Other ungulates generally do not penetrate this waterless habitat.

On the north bank of the Kuiseb a network of ruggedly eroded gulleys and washes drops from the gravel plains down into the river course. Small shrubs and grasses and occasional trees (*Acacia erioloba* and *A. reficiens*) are more common here but are not abundant anywhere. This is the preferred habitat of mountain zebra. Some gemsbok and springbok move into this area after seasonal rains, but during this study few were observed.

Between these two strikingly different areas the seasonally dry Kuiseb River has incised a deep narrow gorge that extends from above the Kuiseb-Gaub confluence to Nareb. Down-river the canyon is less marked as it gradually becomes wider and flatter. In the gorge there is little vegetation except for isolated wild fig trees (*Ficus sycomorus*) and irregular clumps of acacias. Down-river from Nareb the acacia dominated (*A. albida* and *A. erioloba*) riparian forest becomes progressively more dense (Fig. 1).

There are two important resources for ungulates in the Kuiseb River. Pods and leaves of the acacias are abundant in the lower parts of the study area, and this is where gemsbok congregate, especially during the dry summer months when food resources in the dunes decline (Hamilton et al., 1977; Tilson, in prep.). Higher up the Kuiseb, particularly in the gorge, food resources are scarce, but water is freely available in irregularly spaced pools which are permanent. These pools are recharged from seasonal floods that originate in the central highlands and escarpment 250–400 km eastwards. Here gemsbok are replaced by mountain zebra that feed on the plains but descend the gorge at night to drink. Three other antelope species are found along the Kuiseb River course, but they constitute only a fraction of the ungulate biomass (Table 1). Klipspringers, *Oreotragus oreotragus*, are restricted to the canyon slopes; steenbok, *Raphicerus campestris*, are confined to the riparian forest; and springbok, *Antidorcas marsupialis*, occasionally visit the river between Gobabeb and Homeb (Tilson and Kok, in preparation).

<table>
<thead>
<tr>
<th>TABLE 1: Estimated ungulate biomass in the study area (Fig. 1) calculated from an aerial census (Erasmus and Eyre, 1976) and from road censuses (Tilson and Kok, in preparation) during 1976/77.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Biomass/3,080 km²</strong></td>
</tr>
<tr>
<td>Mountain zebra</td>
</tr>
<tr>
<td>Gemsbok</td>
</tr>
<tr>
<td>Springbok</td>
</tr>
<tr>
<td>Klipspringer</td>
</tr>
<tr>
<td>Steenbok</td>
</tr>
<tr>
<td><strong>Total</strong></td>
</tr>
</tbody>
</table>
Both Kruuk (1972) and Bearder (1977) have shown that the identification of prey hairs in spotted hyaena scats gives a relatively accurate assessment of the frequencies that different prey are consumed. Over a period of 12 months we collected a total of 595 fresh samples from three localities along 100 km of the Kuiseb River. The largest number was from the site called Nareb. They were air-dried, brushed to remove sand particles adherent to the surface, then pulverised and sifted in the laboratory at Gobabeb. The remaining hair and other items were transferred to numbered vials and later identified under a binocular microscope (magnifications 16–32x) by comparing them with a reference collection of hair types representing potential prey in the Namib (see Kruuk, 1972). Our samples were well represented with hundreds of hairs from only one species of prey in each scat. From the 595 samples 88.5% (527) had one hair type, 2.7% (16) had none, and only 8.4% (52) had two or more hair types. This analysis was also facilitated by the relatively few prey species available to hyaenas in the study area, in contrast to other study sites.

Part of the substrate particles cemented inside each sample was kept with the associated hair. These particles were compared under a binocular microscope (×32) with a reference collection of substrate particles from the three habitats described above and in Table 2. Dune sand is the most distinctive substrate because of its orange colour and rounded granules. Substrate particles from the plains and river channel are less distinct but can be separated by a combination of characters (Table 2). With this method we could establish within reasonable limits where the prey was consumed.

Age and sex determinations of gemsbok and mountain zebra carcasses were based on skulls examined or retrieved from carcasses before the hyaenas carried them away. Mountain zebra show a clear sexual dimorphism in permanent canines, which are well developed in males but absent or rudimentary in females. Age classes closely follow a sequential eruption and subsequent wearing of deciduous and permanent teeth (Joubert, 1972a). Gemsbok were aged in a similar manner, but horn shape and size were used to determine sex (O. Kok, personal communication).

Analyses of the social organisation of hyaenas in the Namib and their feeding strategies will be presented elsewhere. For the present purpose, the study population of 17 individually identified hyaenas (13 adults and 4 offspring) can be divided into three separate groups. These groups may represent extended family units of a single clan or clans as described by Kruuk (1972). Each group maintained a relatively stable social and spatial organisation for most of this study. Some individuals, especially young males, showed great mobility and exchanged groups. However, group foraging areas were mutually exclusive, separated by distances of 10–20 km (Fig. 1). By plotting the outermost localities where hyaenas fed, we could calculate the approximate foraging area of each group. These should not be construed to represent individual or group home ranges, which are far larger. Thus, the presence of transients, which may feed in one foraging area, then move to another group and use its latrines, may influence our results but not sufficiently to obscure the general trends we establish here.

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**TABLE 2:** Major characteristics of surface sand from the three habitats in the study area. Percentages of constituents are based on crude counts.

<table>
<thead>
<tr>
<th>Region</th>
<th>Sand type</th>
<th>Colour</th>
<th>Shape</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>DUNES</td>
<td>Quartz stained with iron oxide and traces of feldspar, garnet, mica</td>
<td>orange</td>
<td>polished surface, sub-rounded to sub-angular</td>
<td>100</td>
</tr>
<tr>
<td>RIVER</td>
<td>Mica/mica-schist</td>
<td>shiny black</td>
<td>flat</td>
<td>20–30</td>
</tr>
<tr>
<td></td>
<td>Granite, garnet and feldspar</td>
<td>opaque orange</td>
<td>rounded to well-rounded</td>
<td>20–30</td>
</tr>
<tr>
<td></td>
<td>Quartz stained with iron oxide</td>
<td>orange</td>
<td>rounded to well-rounded</td>
<td>20–30</td>
</tr>
<tr>
<td>PLAINS</td>
<td>Quartz, unstained</td>
<td>white</td>
<td>well-rounded to angular</td>
<td>20–30</td>
</tr>
<tr>
<td></td>
<td>Mica, fine</td>
<td>shiny black</td>
<td>flat</td>
<td>10–20</td>
</tr>
<tr>
<td></td>
<td>Granite, garnet and feldspar</td>
<td>opaque orange</td>
<td>sub-rounded to sub-angular</td>
<td>10–20</td>
</tr>
<tr>
<td></td>
<td>Quartz stained with iron oxide</td>
<td>orange</td>
<td>sub-rounded to angular</td>
<td>20–30</td>
</tr>
<tr>
<td></td>
<td>Quartz, unstained</td>
<td>white</td>
<td>angular to very angular</td>
<td>40–60</td>
</tr>
</tbody>
</table>
3 RESULTS

3.1 Prey items in the diet

Skulls, horns and large vertebrae were usually the only parts of a carcass to remain after hyaenas had fed, and even these were often carried away. Nevertheless, a number of carcasses was found by following tracks of hyaenas through the sand-dunes (see Elof, 1964) and by random searching of the study area. The evidence indicated that hyaenas fed almost exclusively on gemsbok and mountain zebra, and that the relative frequency of these two prey species was significantly different between groups (see below). To supplement these observations 595 scats were analysed (Table 3). Viewed collectively, gemsbok were the single most important prey item for hyaenas in the area, accounting for 79.6% of the total sample. Mountain zebra were a distant second at 12.6%, but together these two ungulates accounted for 92.2% of the combined diets. The smaller antelopes (springbok, steenbok and klipspringer) constituted only 2.2% of the total diet, with the remaining 5.6% contributed by small miscellaneous mammals and ostriches. The relatively diverse spectrum of food items in the hyaenas' diet, relative to the species available (see Stuart 1975), indicates how opportunistic hyaenas can be in feeding on what are probably scavenged food items. But the predominance of gemsbok and mountain zebra suggests that the hyaenas are concentrating on larger sized prey, which agrees with other studies on hyaena feeding habits. In the open savannah of East Africa Kruuk (1972) documented wildebeest, Connochaetes taurinus, and zebra, Equus burchelli, as the major prey. In a woodland habitat of South Africa Bearder (1977) reported wildebeest, impala, Aepyceros melampus, and lion-killed giraffe, Giraffe camelopardalis, as the major food sources.
TABLE 3: Distribution of prey hairs from the three hyaena groups in the study area.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Natab</th>
<th>Nareb</th>
<th>Zebra Pan</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>%</td>
<td>N</td>
<td>%</td>
</tr>
<tr>
<td>MAMMALIA</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gemsbok (Oryx gazella)</td>
<td>67</td>
<td>93.1</td>
<td>389</td>
<td>82.2</td>
</tr>
<tr>
<td>Mountain zebra (Equus zebra hartmannae)</td>
<td>—</td>
<td>—</td>
<td>47</td>
<td>9.9</td>
</tr>
<tr>
<td>Springbok (Antidorcas marsupialis)</td>
<td>2</td>
<td>2.8</td>
<td>3</td>
<td>0.6</td>
</tr>
<tr>
<td>Klipspringer (Oreotragus oreotragus)</td>
<td>—</td>
<td>—</td>
<td>7</td>
<td>1.5</td>
</tr>
<tr>
<td>Steenbok (Raphicerus campestris)</td>
<td>—</td>
<td>—</td>
<td>2</td>
<td>0.4</td>
</tr>
<tr>
<td>Domestic goat (Capra sp.)</td>
<td>2</td>
<td>2.8</td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td>Spotted hyaena (Crocuta crocuta)</td>
<td>—</td>
<td>—</td>
<td>3</td>
<td>0.6</td>
</tr>
<tr>
<td>Genet (Genetta genetta)</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td>Hare (Lepus capensis)</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td>Hyrax (Procavia capensis)</td>
<td>—</td>
<td>—</td>
<td>1</td>
<td>0.2</td>
</tr>
<tr>
<td>Rodentia</td>
<td>—</td>
<td>—</td>
<td>9</td>
<td>1.9</td>
</tr>
<tr>
<td>Unknown²</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>AVES</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ostrich (Struthio camelus)</td>
<td>72</td>
<td>1.4</td>
<td>9</td>
<td>1.9</td>
</tr>
<tr>
<td>Total Samples</td>
<td>71</td>
<td>460</td>
<td>64</td>
<td>595</td>
</tr>
</tbody>
</table>

¹These specimens presumably came from a Topnaar settlement near Homeb.
²Hair specimens tentatively identified as Poecilogale albinucha by the Mammal Research Institute, Pretoria (J. Skinner, pers. comm.).

Hyenas are known to have catholic tastes and will consume a variety of animal, vegetative and inorganic objects (Van Lawick—Goodall and Van Lawick, 1970; Kruuk, 1972; Bearder, 1977). Pieces of rubber, plastic and cloth were occasionally found in regurgitations, but hyenas in the Kuiseb River are relatively isolated and have little exposure to such material. Stuart (1976) reported that spotted hyaenas in the Namib occasionally eat the spiny fruit of the narra (Acanthoscypha horrida), a cucumber that grows in the sand-dunes. Although we did find narra seeds in two regurgitations, this practice is not considered to be widespread or frequent. The seeds of acacias and fragments of leaves, grass stems and twigs were present in half of the samples (50.5 %), but we believe these items were derived from eating the rump of the prey rather than purposely eaten to aid regurgitation (Bearder, 1977).

One example of cannibalism was observed, and the presence of numerous hyaena hairs in three samples (0.5 %) from the area where it occurred were later noted (Table 3). In another 7.5 % of the samples a few hyaena hairs were found, but these probably originated from hyaenas licking one another and themselves (Kruuk, 1972). In other areas cannibalism has also been reported (Pienaar, 1969; Van Lawick—Goodall and Van Lawick, 1970; Kruuk, 1972) but it is relatively rare.

3.2 Prey variation between groups

Kruuk (1972) reported that spotted hyaenas in East Africa live in large communities called clans comprised of 40 to 80 individuals. These clans aggressively defend territories that are marked along the boundaries with scats (= latrines) and with anal scent marking (= pasting). In the Ngorongoro Crater, where prey are numerous and year-round residents, clans and territories are relatively stable, but in the Serengeti, where there are large temporary fluctuations in food supply when the ungulate migrations occur, the clan system is disrupted and territories less precisely defined. Rather than marking boundaries, hyaenas in the Serengeti mark along certain routes which they travel over long distances in search of game. Hyaenas in the Namib are similar to those in the Serengeti. Near dens and latrines, and the trails leading from them, latrines are conspicuous, but peripheral boundaries are not well marked. We found three general areas containing latrines close to dens of three different hyaena groups (called the Natab, Nareb and Zebra Pan groups (Fig. 1)).

We were able to distinguish roughly the foraging areas of these three hyaena groups. As some individuals occasionally transferred between groups, we use foraging areas to define the space in which a particular
group, rather than an individual, confined its foraging activities. Boundaries of foraging areas represent the outermost sites where the group was observed feeding on a carcass (Fig. 1). Group boundaries were separated by up to 15 km, so foraging areas were considered to be mutually exclusive. Each foraging area contained at least one den or lair near open water along the Kuiseb River. Because of the distances between locations (20–35 km) and the relative stability of hyaena groups living there, we believe it is reasonable to presume that prey hairs from separate latrines reflect what hyaenas are feeding on in that foraging area.

The frequency of prey items in the diet samples of the Natab (6 hyaenas), Nareb (4 hyaenas) and Zebra Pan (7 hyaenas) groups is presented in Table 3. Considering only the main prey, gemsbok and mountain zebra, there is a significant dietary difference among the three groups ($t^2 = 2.25$, $p<0.01$). Hyaenas at Natab had a diet comprised almost exclusively of gemsbok (93.1%) but mountain zebra were conspicuously absent. At Nareb gemsbok (82.2%) were still the most important prey, but some mountain zebra (9.9%) were represented in this group’s diet. In contrast, Zebra Pan hyaenas had about equal numbers of gemsbok (50.0%) and mountain zebra (42.1%) in their diet. These differences can be explained by the differential distribution of the two prey species within the respective hyaena foraging areas.

Gemsbok occur throughout the study area but reach their largest numbers in the north–eastern areas of the Namib near Ganab (Fig. 1). They also are the only large ungulate that range far into the dunes. Towards the end of the dry season part of the dune population moves into the Kuiseb River, mostly between Natab and Hudaab. In contrast, mountain zebra do not range down river from the Gorob canyon confluence. Most are found in the vicinity of Zebra Pan and parts north along the river’s course. Both gemsbok and mountain zebra show some seasonal movements, but nowhere in their range are they ever completely absent. The Nareb area represents the zone of overlap for these two ungulates as well as for klipspringer and steenbok (Tilson, in preparation).

### 3.3 Seasonal variation in prey

After the rains fall in the Namib gemsbok and mountain zebra leave the confines of the Kuiseb River to disperse into the dunes and plains, and hyaenas must travel further afield to find them. This seasonal adjustment is not reflected in an analysis of hair types. The only evidence of seasonal change in diet was the presence of gemsbok calves (distinguished by their distinctive postnatal coloration) during the months of November through January (Fig. 2). Gemsbok do not have a short, sharp birth season like wildebeest (Estes, 1976), but they do show a peak in November (Hamilton et al., 1977). After about four months calves closely resemble adults in coloration and could not be distinguished by hair type from adults. For similar reasons mountain zebra foals were not separated from adults in the analysis. Thus, our values most likely under-represent the percentage of immature animals in the overall diet.

In other areas the consumption of calves is a more striking seasonal phenomenon (wildebeest in East Africa, Kruuk, 1972; impala in South Africa, Bearder, 1977). In Ngorongoro Crater wildebeest calves accounted for over 60% of the hyaenas’ diet during the short birth season (Kruuk, 1972). Predation on calves has promoted breeding synchrony and the formation of large aggregations of wildebeest, partly to satiate the predators and partly to create confusion to prevent one-day-old calves from being detected (Estes, 1976). Aside from the restrictions of methodology cited, the less pronounced emphasis on calves in the Namib hyaena diet may be attributed to the low density and wide dispersion of the prey populations. A greater emphasis on calf predation would be expected when gemsbok congregate at resource rich areas during severe droughts, such as observed by Hamilton et al. (1977).

### 3.4 Age and sex of prey

In our study we never observed hyaenas killing their prey, but we did find 29 gemsbok and 26 mountain zebra carcasses. About half of these were killed by hyaenas, and at least four were natural deaths (Tilson, in prep.).

The age and sex categories of gemsbok and mountain zebra consumed by hyaenas are presented in Table 4. The sex ratio of adult gemsbok (over one year of age) was 1.9 males for every 1.0 female. But in a sample of 2884 gemsbok counted in the Namib gravel plains no significant deviation from a 1:1 sex ratio was found (O. Kow, personal communication). Even though male gemsbok outnumbered females in the carcass counts,
the difference was not significant \( X^2 = 2.79, p<.10 \). In contrast, significantly more female mountain zebra were eaten (0.4 males vs. 1.0 females, \( X^2 = 3.85, p<.05 \)) even though these animals have nearly equal sex ratios in the wild (Joubert, 1972b).

The age class separation of both gemsbok and mountain zebra shows that old animals (over eight years old) were more often eaten than young ones (70.1 % vs. 29.1 %, Table 4). These figures are significant for gemsbok \( (X^2 = 9.97, p<.001) \) but not for mountain zebra \( (X^2 = 1.38, p>.30) \). If only adults are considered then even the mountain zebra figures are significant \( (X^2 = 5.75, p<.02) \). This sample may be biased towards older individuals, because the probability that young skulls will remain intact is much less than that for adult skulls. However, within the adult categories (over one year of age) older animals still form the greatest percentage. Animals from 1–8 years constituted 23.8 % of the mountain zebra and 12.5 % of the gemsbok contrasted to 76.2 % and 87.5 %, respectively, for individuals 8–16 years old. We found only a single mountain zebra in the 1–4 year old category. The evidence presented here suggests that hyaenas are selecting older individuals over younger, but the contribution of immature calves and foals is probably underestimated.

\[
\begin{array}{c|c|c|c|c}
\hline
\text{Age (years)} & \text{Gemsbok} & \text{Mountain zebra} \\
\hline
\text{Immature} & & & & \\
1 & 2(6.9) & 1(3.5) & 1(3.9) & 4(15.4) \\
\text{Adults} & & & & \\
1–4 & 0 & 0 & 0 & 1(3.9) \\
4–8 & 2(6.9) & 1(3.5) & 2(7.7) & 2(7.7) \\
8–12 & 5(15.7) & 8(27.6) & 3(11.5) & 8(30.8) \\
12–16 & 2(7.7) & 3(11.5) & & \\
\hline
\text{Total} & 19(65.5) & 10(34.5) & 8(30.8) & 18(69.2) \\
\end{array}
\]

### 3.5 Site of prey consumption

Different prey species showed associations with different substrate types, even though a considerable amount of overlap was evident (Fig. 3). The Natab hyaenas, which fed almost exclusively on gemsbok (93.1 %, Table 3), consumed over half of their prey on a sandy substrate, presumably in the dune fields south of the Kuiseb. Another third of the gemsbok were eaten in the vicinity of the river, and only a few on the gravel plains (Fig. 3A). At Nareb, where gemsbok again were the predominant food item (82.2 %) for hyaenas, a similar relationship prevailed (Fig. 3B). The small number of mountain zebra (9.9 %) eaten at Nareb showed nearly equal values for all three habitats. In contrast to these two groups, hyaenas at Zebra Pan consumed the greater part of their prey on the gravel plains or in the river-bed. Only a fraction of the gemsbok were associated with a dune sand substrate (Fig. 3C). These patterns of prey type and substrate associations support the observations on each group's foraging area depicted in Fig. 1. Hyaenas at Natab and Nareb concentrate their foraging activities in the river and sand-dunes to the south where gemsbok congregate. At Zebra Pan the gravel plains and areas adjacent to the river are more commonly used by hyaenas.

The distribution of substrate associations for the combined diets of the hyaena population is presented in Fig. 3D. Aside from some minor differences, the combined values reflect the general trends shown for the Nareb group, which was the most intensively sampled area (77.5 % of the total 595 samples). Excluding mixed samples (where two habitats are represented) the following trends were established. Of the 477 gemsbok, a significant number \( (X^2 = 20.46, p<.01) \) were consumed in the dunes (50.5 %).
compared with the riverine habitat (35.6 %) or gravel plains (13.8 %). A significant number of the 59 mountain zebra samples (X² = 21.13, p<.01) came from the gravel plains (50.9 %) rather than the riverbed (35.6 %) or dune field (13.5 %), a converse relationship to the gemsbok trend.

4 DISCUSSION

The Kuiseb River and its surroundings in the central Namib Desert do not support an abundant or diverse mammalian community (Coetzee, 1969; Stuart, 1975). This is especially true of large ungulates and their predators. Outside of the narrow riparian forest of the Kuiseb River food resources are sparse and patchy in distribution due to the unpredictable and low rainfall regime that characterises the Namib (Seely and Stuart, 1976). The most abundant large ungulates in the central Namib, gemsbok and mountain zebra, are more common in the eastern and northern parts of the Namib-Naukluft Park, but nowhere do they reach the enormous numbers of the savannah or woodland habitats described elsewhere. In East Africa the estimated biomass of the ungulate population is approximately 55 (Serengti Plains) to 120 (Ngorongoro Crater) times greater (Kruuk, 1972) than in the Namib (Table 1); in a woodland habitat of South Africa (Timbavati) it is about 35 times as great (Bearder, 1977). Thus, the low species diversity and impoverished numbers of potential prey in the Namib, coupled with the lack of competition from large predators, distinguishes this desert from other localities where spotted hyaenas have been studied. Despite these dissimilarities, hyaenas in the Namib have a diet that is not much different from that of hyaenas in East Africa. There, medium sized ungulates (wildebeest and zebra) are more frequently taken than larger (buffalo) or smaller ones (gazelles). Also, hyaenas in East Africa show no clear preference for either wildebeest or zebra, and the presence of these species in the annual diet corresponds closely with their relative abundance (Kruuk, 1972). An analogous relationship between gemsbok and mountain zebra occurs in the Namib. In southern Africa (Timbavati) impala and lion-killed giraffe were the two most important food items for hyaenas (Bearder, 1977). Thus, where hyaenas are the sole or dominant predator in the system their diet may reflect the relative abundance of medium sized ungulates in the area, but where they are sympatric with other large carnivores, especially lions, this relationship is obscured or totally absent.

The manner in which most Namib prey was obtained is not well documented. There was no evidence of large scale mortality of gemsbok or mountain zebra through drought or starvation during the period of this study; so hyaenas were either finding a large number of animals which had died through natural causes, or they were responsible for killing a number of animals themselves. Several lines of evidence suggest the latter.

In 1976 over 125 mm of rain fell in most parts of the research area (Gobabeb meteorological records). This was a sevenfold increase over the annual average, and as a result range conditions improved dramatically. The general physical condition of gemsbok also improved. For comparison, we used a system described by Hamilton et al. (1977) to quantify the apparent relative physical condition of individual gemsbok censused in the Kuiseb. On a scale of 1 (= good) to 5 (= poor) a significant decline in the condition of the herd (male/female values decreased from 1.2/1.8 to 2.7/3.7; p<.01) occurred in late summer 1972/73, and considerable mortality resulted from a decrease in food and water resources (Hamilton et al., 1977). In the same area during late summer 1976/77 the general condition of the herd was maintained at higher values (male/female values = 1.2/1.5), and very little natural mortality was observed. No comparable figures are available for mountain zebra or springbok, but general observations suggest their condition paralleled that of gemsbok. It is unlikely that any stable population of hyaenas could subsist entirely on random and unpredictable instances of natural death occurring in such widely dispersed and relatively healthy populations of prey.

If gemsbok and mountain zebra have nearly equal sex ratios how can the differential selection of one sex be reconciled? A similar pattern was noted in East Africa by Kruuk (1972). Adult male wildebeest were killed twice as often as females in the Serengeti, but male/female ratios were almost equal in Ngorongoro. The cause of the difference in mortality between males and females could not be explained. We believe the difference in mortality between male and female gemsbok may result from intrasexual aggression that is more prevalent among males than females. In 1976/77 monthly censuses of the Kuiseb River, 479 gemsbok were counted. Of 230 adult males 15 (6.5 %) were hobbling on injured legs. Horn punctures in the ribs, flanks or buttocks were noted on about half of them. Also, 35 (15.2 %) males were missing part or all of one horn, and another 8 (3.5 %) were missing both horns. Among the 249 females 3 (1.2 %) were missing part of a horn, and only one was observed limping. The loss of horns and other injuries to males presumably were inflicted during intermale combat in order to gain access to females or to certain key resources (see Hamilton et al., 1977). In the absence of other evidence, it is suggested that such injuries could influence an animal's ability to flee or to deter hyaenas during encounters, and may explain why male gemsbok outnumber females in the carcass counts.

The selection of female mountain zebra over males requires a different explanation. In East Africa Kruuk (1972) noted that hyaenas killed more female zebra in both the Serengeti and the Ngorongoro, which he attributed to the zebra's antipredator behaviour. Zebra stallions aggressively defend their family units from attacks by hyaenas, while mares do not. The greater aggressiveness of stallions can be an effective deterrent
to hyaenas, and only by separating a mare from the family unit can hyaenas be successful (Kruuk, 1972). Mountain zebras are similar in social organisation and behaviour and have nearly equal sex ratios in the Namib (Joubert, 1972b). This alone may explain the differential selection of females over males.

The greater number of old individuals in the carcass counts, regardless of sex, suggests that hyaenas scavenge as well as hunt in the Namib. During severe droughts, as observed in the summer of 1972/73 (Hamilton et al., 1977), natural mortality of the prey population may enable hyaenas to rely solely on scavenging. But during periods of better range and herd condition, hunting would be necessary to maintain a resident population of hyaenas. As Kruuk (1972) points out, predation by hyaenas is not merely supplementary to other sources of mortality but interacts closely with them. If alternate causes of mortality are numerically important, then predation merges with them, and hyaenas take what has died already. If other causes of mortality are absent, then hyaenas act as independent mortality agents.

5 ACKNOWLEDGMENTS

This research was funded by the CSIR, Transvaal Museum and the Nature Conservation and Tourism Division of South West Africa. The latter also provided use of its facilities and permission to work in the Namib-Naukluft Park. We wish to thank C. G. Coetzee, Stau Museum/Windhoek, for providing the reference collection of prey hairs and Prof. John Skinner, Mammal Research Institute/Pretoria, for identifying several unknown hair types. Andrew Watson, Oxford University, is thanked for classifying the substrate types, and Gert Cloete for assisting in the field. We are particularly grateful to Chris Eyre for sharing his knowledge of hyaena distribution in the park. Drs. Mary Seely and Robert Wharton read an earlier version of this manuscript and offered helpful comments.

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HIRST, S. M.

Joubert, E.

KRUUK, H.

MILLS, M. G. L.

PIENAAR, U. de V.

SEELY, M. K., and STUART, P.

STUART, C. T.

VAN LAWICK-GOODALL, J. and VAN LAWICK, H.
Waders (Charadrii) and other coastal birds of the Diamond Coast and the islands off South West Africa

by

J. Cooper, H. G. Robertson

Percy FitzPatrick Institute of African Ornithology,
University of Cape Town,
Rondebosch, 7700, South Africa

and

P. D. Shaughnessy

Sea Fisheries Institute,
P. O. Box 251,
Cape Town, 8000, South Africa

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ABSTRACT

Counts of waders (Charadrii) and other coastal birds (excluding gulls Lorus spp.) are given for the islands off South West Africa, and bays in the adjacent mainland coastline. A total of 3460 birds was counted during November – December 1978 of which 2467 were waders. Palearctic migrants formed 76.3 % of the waders. The most abundant wader species on the islands were the turnstone Arenaria interpres and the black oystercatcher Haematopus moquini which together formed 91.9 % of all waders. Lüderitzbucht supported a more varied assemblage of waders (total 1203) than the islands, the curlew sandpiper Calidris ferruginea being the most abundant. Non-waders were primarily black-necked grebes Podiceps nigricollis. Extensions to the known breeding range of the black oystercatcher and range of the black-necked grebe at sea are given. It is suggested that overwintering turnstones may move to relatively sheltered waters.
1 INTRODUCTION

Recently, surveys have been undertaken to assess the numbers of waders (Charadrii) and other coastal birds on parts of the coast-line of southern Africa, and to make recommendations for the protection of important areas. (Cooper, et al. 1976; Summers and Cooper 1977; Summers et al. 1977; Underhill and Whitelaw 1977; Whitelaw et al. 1978).

This paper reports on counts of waders (Charadrii) and other coastal birds on the islands off South West Africa and bays in the adjacent mainland coast-line, the ‘‘Diamond Coast’’, and adds to the body of knowledge of the birds of the southern African coast-line.

2 STUDY AREA AND METHODS

The islands off South West Africa occur close inshore both north and south of Lüderitz from 24°15’ to 27°15’S (Figs 1 and 2). These islands, generally small and barren of vegetation, are described by Rand (1963) who gives details on their breeding seabirds but little information on shorebirds. During November — December 1978 J. C. and H. G. R. visited all the islands off South West Africa (with the exception of Hollamsbird Island (24°38’S, 14°31’E) during a combined Sea Fisheries Branch—FitzPatrick Institute expedition to census breeding seabirds. Counts of waders and other coastal birds, including birds close inshore, were made on all islands visited by walking the length of the coast-line. In addition, birds on several small rocks were counted from a boat. Counts were also made in Lüderitzbucht (Fig. 2). Incidental counts made by P. D. S. for several rocks and in bays on the mainland coast-line over the period 1974/79 have been included. Where relevant, information from the literature is included. All species of birds occurring on the coast-line were counted at all localities, with the exception of gulls. Censuses of breeding kelp gulls Larus dominicanus will be reported elsewhere.

3 RESULTS

Counts at each locality visited in November — December 1978 are given in Table 1; incidental counts by P. D. S. are provided in Table 2. A total of 3,460 birds was counted during the main survey of which 2,467 (71.3 %) were waders (Charadrii). Lüderitzbucht had 1,228 birds or 35.5 % of the total. Palaeartic waders made up 76.3 % of the total numbers of waders counted. The most abundant species was the turnstone Arenaria interpres which made up 35.4 % of the wader population. The wader population of the islands consisted of mainly turnstones and black oystercatchers Haematopus moquini, which together formed 91.9 % of all waders present. Lüderitzbucht supported a more varied assemblage of waders (total 1,203), the most abundant being the curlew sand-piper Calidris ferruginea. Turnstone, knot C. canutus and sanderling C. alba, together with curlew sandpipers, made up 76.0 % of the wader populations of the bay. A single terek sandpiper Tringa terek was seen by P. D. S. in Lüderitzbucht on 18 October 1976 and one curlew Numenius arquata on 3 August 1974 at the same locality. Becker (1965) recorded a kittlitz’s plover Charadrius perspicillatus and a single greenshank T. nebularia in Lüderitzbucht on 14 February 1965.

The non-wader population (excluding gulls) consisted mainly of black-necked grebes Podiceps nigricollis (79.0 %). Approximately 250 greater flamingoes Phoenicopterus ruber, mainly juveniles, were seen in Lüderitzbucht by P. D. S. on 18 October 1976 and on 5 August 1977. Becker (1965) recorded a single caspian tern Sterna caspia in Lüderitzbucht on 12 February 1965 and P. D. S. observed one in the same bay on 3 August 1974.

Swift terns Sterna bergii bred in winter within the area surveyed (Cooper et al. 1977) and the number seen (180) in November — December 1978 is less than the winter population.

4 DISCUSSION

Whitelaw et al. (1978) counted 83,069 birds (including gulls) on approximately 300 km of coast-line centred on Walvis Bay, South West Africa. The majority of these birds occurred in the sheltered habitats of Walvis Bay and Sandvis. They included a count for Elizabeth Bay (Fig. 1) of 525 waders but otherwise concluded that the coast-line between Lüderitz and the Orange River (28°38’S, 16°26’E) supported few birds. However, this coast-line is in a protected diamond mining area, and has not yet been adequately surveyed for coastal birds. Hotentots Bay (Fig. 1) supported a large number of waders when visited in December 1977 (P. G. Johnson pers. comm.). The results given here show that Lüderitzbucht and the islands off South West Africa do support reasonable numbers of coastal birds.

The numbers (total 433 counted) of black oystercatchers on some South West African islands are given by Summers and Cooper (1977). We counted 477 on more islands. However, numbers of black oystercatchers on islands vary with time of year and state of tide (Summers and Cooper 1977). On 6 December 1978 Pomona Island contained 29 black oystercatchers at high tide. The next day, at low tide, only seven were present. One of us (P. D. S.) has seen an oystercatcher flying from the mainland to Possession Island. Table 3 gives counts of oystercatchers for five islands made in winter 1977 and together with the data given in Summers and Cooper (1977), show the large variations that can occur. P. D. S. in Summers and Cooper (1977) observed a density of 3.6 birds per kilometre on seven kilometres of the mainland at Van Reenen Bay (27°24’S, 15°15’E) (Fig. 1). Elizabeth Bay supported nine birds in three kilometres
(Whitelaw et al. 1978) and Lüderitzbucht contained 17 (Table 1). Oystercatchers were also present at several other bays on the mainland coast-line (Table 2). Thus, the mainland population of oystercatchers opposite the islands is likely to be high.

Summers and Cooper (1977) give the northernmost breeding range of the black oystercatcher as Penguin Island. On 18 May 1977 one of us (J. C.) recorded breeding (C/2) on Seal Island, a small extension to the breeding range (Fig. 2). A nest with three eggs was also recorded on Seal Island on 22 January 1978 (R. W. Weeks pers. comm.). Breeding commences later in South West Africa than in the south-western Cape (pers. obs.) and no nests were found during the main survey. However, birds on Ichaboe and Mercury Islands behaved as pairs and it is likely that the breeding range extends as far north as the coast-line opposite Mercury Island.

A small range extension for the black-necked grebe was also observed with 41 birds counted off Possession Island (Table 1). On 13 January 1978, P. D. S. observed 300 at this locality. Winterbottom (1971) gave Lüderitz as the southern limit of the coastal range in South West Africa.

A total of 179 knot was counted in Lüderitzbucht, a locality not listed by Dick et al. (1976) for this species. Lüderitzbucht contained similar species to other sheltered waters of the west coast of southern Africa (e.g. Langebaan Lagoon (Pringle and Cooper, 1975) and Walvis Bay and Sandvis (Whitelaw et al. 1978)), and
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### Non-Palaearctic waders

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* Recorded by Rand (1949), who also recorded kittlitz plover Charadrius pecuarius and curlew Numenius arquata
+ One seen during May 1977
* recorded by P. D. S. in January 74/79
TABLE 2: Incidental counts of waders (Charadrii) and other coastal birds within the survey area, 1974/78

<table>
<thead>
<tr>
<th>Locality</th>
<th>Marshall Rocks</th>
<th>Dunedin Rocks</th>
<th>Stormvoelbuurt</th>
<th>Grossbaai</th>
<th>Wolf Bay</th>
<th>Atlas Bay</th>
<th>Lady's Rocks</th>
<th>Van Reenen Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>24/1/78</td>
<td>11/1/78</td>
<td>7/74</td>
<td>13/7/74</td>
<td>24/1/76</td>
<td>24/1/76</td>
<td>24/1/79</td>
<td>1/75–77</td>
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</table>

Non-Palaearctic waders

<table>
<thead>
<tr>
<th>Species</th>
<th>Marshall Rocks</th>
<th>Dunedin Rocks</th>
<th>Stormvoelbuurt</th>
<th>Grossbaai</th>
<th>Wolf Bay</th>
<th>Atlas Bay</th>
<th>Lady's Rocks</th>
<th>Van Reenen Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black oystercatcher</td>
<td>0</td>
<td>2</td>
<td>7</td>
<td>c.30</td>
<td>7</td>
<td>5</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
<td>Haematopus moquini</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-fronted plover</td>
<td>0</td>
<td>0</td>
<td>20</td>
<td>4</td>
<td></td>
<td>0</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Charadrius marginatus</td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Total</td>
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<td>27</td>
<td>30+</td>
<td>11</td>
<td>5</td>
<td>0</td>
<td>28</td>
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Palaearctic waders

<table>
<thead>
<tr>
<th>Species</th>
<th>Marshall Rocks</th>
<th>Dunedin Rocks</th>
<th>Stormvoelbuurt</th>
<th>Grossbaai</th>
<th>Wolf Bay</th>
<th>Atlas Bay</th>
<th>Lady's Rocks</th>
<th>Van Reenen Bay</th>
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<tbody>
<tr>
<td>Turnstone</td>
<td>20</td>
<td>50</td>
<td>2</td>
<td>c.100</td>
<td>28</td>
<td>*</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>Arenaria interpres</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grey plover</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>*</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Pluvialis squatarola</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Curlew sandpiper</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>c.100</td>
<td>8</td>
<td>*</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Calidris ferruginea</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Sanderling</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>c.25</td>
<td>c.25</td>
<td>*</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Calidris alba</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Common sandpiper</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>*</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Tringa hypoleucoh</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>Whimbrel</td>
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<td>1</td>
<td></td>
<td></td>
<td>*</td>
<td>0</td>
</tr>
<tr>
<td>Numenius phaeopus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Total</td>
<td>20</td>
<td>52</td>
<td>155</td>
<td>164+</td>
<td>44</td>
<td>5</td>
<td>20</td>
<td>36</td>
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</table>

Non-waders

<table>
<thead>
<tr>
<th>Species</th>
<th>Marshall Rocks</th>
<th>Dunedin Rocks</th>
<th>Stormvoelbuurt</th>
<th>Grossbaai</th>
<th>Wolf Bay</th>
<th>Atlas Bay</th>
<th>Lady's Rocks</th>
<th>Van Reenen Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swift tern</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>c.40</td>
<td>0</td>
<td>0</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>Sterna bergii</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Damara tern</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>c.35</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>S. bataenarum</td>
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<tr>
<td>Cape teal</td>
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<td>0</td>
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<td></td>
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<td></td>
<td></td>
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<tr>
<td>Anas capensis</td>
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<td>0</td>
<td>0</td>
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<tr>
<td>Phoenicopterus ruber</td>
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<td></td>
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<td></td>
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<tr>
<td>Total non-waders</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>c.75</td>
<td>0</td>
<td>0</td>
<td>9</td>
<td>0</td>
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</tbody>
</table>

Total no. birds

<table>
<thead>
<tr>
<th></th>
<th>Marshall Rocks</th>
<th>Dunedin Rocks</th>
<th>Stormvoelbuurt</th>
<th>Grossbaai</th>
<th>Wolf Bay</th>
<th>Atlas Bay</th>
<th>Lady's Rocks</th>
<th>Van Reenen Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>South West Africa</td>
<td>20</td>
<td>52</td>
<td>156</td>
<td>239+</td>
<td>44</td>
<td>5</td>
<td>29</td>
<td>36</td>
</tr>
</tbody>
</table>

* recorded present on other dates by P. D. S.

Five were seen nearby by J. C. & H. G. R. on 28 November 1978 and ca. 50 by P. D. S. on 23 January 1976.
TABLE 3: Counts of waders (Charadrii) on some islands off South West Africa, Winter 1977.

<table>
<thead>
<tr>
<th>Island</th>
<th>kraai</th>
<th>seel</th>
<th>penguin</th>
<th>shank</th>
<th>halifax</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>17/5</td>
<td>18/5</td>
<td>18/5</td>
<td>15/5</td>
<td>19/5</td>
</tr>
</tbody>
</table>

Non-Palaeartic waders

Black oystercatcher
*Haematopus moquini*
2 85 61 6 96
White-fronted plover
*Charadrius marginatus*
0 3 0 4 2
Three-handed plover
*C. tricolor*
0 0 2 0 0

Palaeartic waders

Turnstone
*Arenaria interpres*
4 1 0 9 7
Grey plover
*Pluvialis squatarola*
0 0 0 0 1

wintering by turnstones on the open coast-line is uncommon in the south-western Cape and it is thought that birds move from the open coast-line to Langebaan Lagoon where turnstones are relatively abundant in winter (Pringle and Cooper 1975, 1977). Overwintering by Palaeartic waders, including turnstones, occurs at approximately 25 % of summer numbers on the sheltered coast-line between the Swakop River (22°40'S, 14°30'E) and Walvis Bay (22°59'S, 14°31'E) (Whitelaw et al. 1978, pers. obs.). Turnstones overwintering in South West Africa may also move to sheltered waters. Lüderitzbucht can support quite large populations of overwintering grey plovers: P. D. S. saw more than 80 on 3 August 1974.

The presence of Damara terns *Sternula balaenarum* at Grobbelbucht (Table 2, Fig. 2) suggests that an undiscovered breeding colony may occur nearby. Frost and Johnson (1977) and Siegfried and Johnson (1977) surveyed the area for terns but saw none. However, Clinning (1978) saw birds carrying fish inland at Grossbucht and also considers a breeding colony may exist nearby, and on 8 December 1978 P. G. Johnson (pers. comm.) saw an adult Damara tern carrying a fish inland at the same locality. Damara terns have also been seen in Lüderitzbucht by P. D. S. (two on 20 July 1974 and one on 27 September 1977). It is likely that the Damara terns seen foraging inshore of Marshall Rocks (Table 2, Fig. 1) were from the recently discovered Hottentots Bay colony (Siegfried and Johnson 1977). This colony was found on the salt-pan stretching south of Hottentots Bay approximately seven kilometres from Marshall Rocks (P. G. Johnson pers. comm.).

The islands off South West Africa (with the exception of Shark Island which is joined to the mainland by a short causeway and several of the small rocks) are part of South Africa and fall under the jurisdiction of the Sea Fisheries Institute of the Department of Agriculture and Fisheries. As landing is allowed by permit only, there is little disturbance to the birds. Lüderitzbucht is in a condition similar to its natural state. The rest of the mainland coast-line is a restricted diamond area. It is recommended that the islands continue to be protected and that any development in Lüderitz should not affect the mud flats on which the birds feed.

5 ACKNOWLEDGEMENTS

We are grateful to the Sea Fisheries Institute, Department of Agriculture and Fisheries, South Africa, for making the survey possible. Especially, we wish to thank R. J. M. Crawford and P. A. Shelton for arranging the survey and Skipper M. M. du Toit, *Malagasy II*, for so efficiently transporting us between the islands. H. A. van der Heyde helped with counts and gave important logistical support. P. D. S. was helped by G. L. Shaughnessy when making a number of counts. We thank P. G. Johnson for his observations of Damara terns and other shorebirds on the “Diamond Coast”.

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FROST, P. and JOHNSON, P.

PRINGLE, J. S. and COOPPER, J.

PRINGLE, J. S. and COOPPER, J.

RAND, R. W.
SIEGFRIED, W. R. and JOHNSTON, P.  

SUMMERS, R. W. and COOPER, J.  

SUMMERS, R. W., COOPER, J. and PRINGLE, J. S.  

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1978: Waders (Charadrii) and other birds on the Namib Coast: counts and conservation priorities. Medoqua, 11: 137 - 150.

WINTERBOTTOM, J. M.  
Three additions to the marine fish fauna of southern Africa

by
M. J. Penrith
State Museum,
Windhoek, South West Africa

Received: 6 July 1979

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ABSTRACT

Three species of fish belonging to the families Polynemidae and Scorpaenidae are recorded from the southern African faunal area for the first time.
1 INTRODUCTION

The limits of the southern African marine faunal area have been defined by a number of authors. For fish the recent limitation of the area to the seas off southern Africa from the Kunene River mouth on the west coast to Beira on the east coast (Smith 1975) provides a natural and logical scheme. Within the area, the eastern portion is well known, the western half less so, and the north-western portion, off the northern Namib coast, is almost unknown. There are two main reasons for the low level of knowledge of this region. Firstly, although there has been a large fishery along the coast for many years operating from Walvis Bay, it is only recently that bottom trawling, as opposed to purse-seining, has been started in the area. Secondly, only very limited shore collecting has been done along the coast. The area is difficult to reach, to stay in, and to work in.

Of the three new records from the northern Namib coast noted below, the two scorpaenids were taken by bottom trawl, and the polynemid by shore collecting. It was collected during a visit to the area when netting was possible on only one day in two weeks.

2 POLYNEMIDAE

Galeoides decadaecylus (Bloch), 1795

Material: SMP 1561.

Description

Standard length 183 mm, head 60 mm, eye about equal to snout, both 4 in head. Base of second dorsal subequal to anal base and slightly more than half head length. Dorsal VII + I, 13. Anal III, 13. Pectoral free rays 8 each side.

The single example is in rather poor condition after being beach-rolled when the gill-net was washed ashore, but the 8 short free pectoral rays clearly identify the species and prevent confusion with other members of the family in the eastern Atlantic or western Indian oceans.

Distribution

Galeoides decadaecylus has a wide distribution in the eastern Atlantic. In the north the species reaches the western extremity of the Mediterranean (Monod 1973) and has been recorded southwards to Baia dos Tigres (Poll 1959; Penrith 1978). Although the present record extends the species range only about 100 km southwards, it is the first record of G. decadaecylus in the southern African faunal area (as defined by Smith 1975). Although only one example was obtained, the species is probably not uncommon south of the Kunene River. It was the only teleost taken in the single gill-netting attempt made during a visit to the area in October 1978.

3 SCORPAENIDAE

3.1 Neomerinthe folgori (Postel & Roux) 1964

Material: SMP 1560.

Description

Standard length 272 mm. Body proportions as in table 1. Dorsal XII, 11. Anal III, 5. Pectoral 17 right, 18 left. Upper 2 rays simple, next 7 branched, rest simple. Tubed lateral line scales 29. Two well-developed simple preorbital spines over maxilla, suborbital ridge well-developed, with many small spines and spine clusters. Supplemental preopercular spine. Three preopercular spines, first the best developed. In general head spines are simple.

Colour pattern after preservation (Plate 1) much as shown by Postel & Roux (1964, Figure 1). Dark tip of caudal present. Fresh (frozen) colour red/orange with darker patches.

The present specimen agrees well with previous descriptions (Postel & Roux 1964; Eschmeyer 1969). Where differences occur, as in the reduced subdivision of head spines relative to Eschmeyer's detailed description, this is probably related to the size difference (272 mm as opposed to 340 mm).

<table>
<thead>
<tr>
<th>TABLE 1: Body proportions as % of standard length for the known examples of Neomerinthe folgori.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard length (mm)</td>
</tr>
<tr>
<td>----------------------</td>
</tr>
<tr>
<td>Head</td>
</tr>
<tr>
<td>Eye</td>
</tr>
<tr>
<td>Snout</td>
</tr>
<tr>
<td>Interorbital</td>
</tr>
<tr>
<td>Depth</td>
</tr>
<tr>
<td>Depth, caudal peduncle</td>
</tr>
<tr>
<td>Jaw</td>
</tr>
<tr>
<td>Predorsal</td>
</tr>
</tbody>
</table>
Distribution

*Neomerinthe folgori* has previously been recorded only from West African waters, Mauritania (Cervigon 1960) and Cape Verde Islands (Postel & Roux 1964) in 180–310 metres. The present record extends the range some 2,900 nautical miles southward. The species is probably much more widely distributed than the records suggest. Eschmeyer (1969) has suggested that it is possibly a rough bottom living species, a habitat type that has been little studied on the African west coast. Although trawled, the present example was taken over rough ground in a reinforced trawl-net.

*Neomerinthe folgori* is not listed in the keys to West African fishes of Blache *et al.* (1970).

3.2 *Pontinus leda* Eschmeyer, 1969

Material: SMP 1562.

Description

Standard length 198 mm. Body proportions as percentage of standard length: head 50.5 %, eye 12 %, snout 15 %, interorbital 3.5 %, depth 39 %, jaw 26 %, predorsal 44 %, 2nd dorsal spine 12.5 %, Dorsal XII. 9, Anal III, 4, Pectoral 18, all rays simple. Tubed lateral line scales 23, vertical scale rows 41.

Preorbital with 2 spines overhanging maxilla, second larger and pointing posteriorly. Suborbital with 4 spines, first very small. Five propectoral spines plus supplemental spine. Third propectoral spine largest. Very small upper posttemporal spine on left side.

Eschmeyer (1969) noted two differences between *Pontinus accraensis* and the related *P. leda*: the presence in the former of elongated second and third dorsal spines and the presence of dark spots on the caudal, features lacking in the latter species. The present example has no elongated dorsal spines but has some scattered dark spots on the caudal.

Preserved colour pattern, especially the dark lateral line and patch on the membrane of the hind half of the spinous dorsal, as described and figured by Eschmeyer, but with some dark spots on the caudal as noted above. Colour before preservation but after freezing shown in Plate 2.

Distribution

Recorded from 2ºS. to 4ºS. (Eschmeyer 1969). Eschmeyer, however, has suggested that many of the more southerly of Poll’s (1959) records of *Pontinus accraensis* (to 16º36’S.) may represent this species. The present record is the first within the southern African faunal area, and extends the range to approximately 18º50’S.
PLATE 2: Pontinus leda, standard length 198 mm. Post mortem coloration (quick frozen after capture).
(Photo: L. Jacobson)

4 ACKNOWLEDGEMENTS

Thanks are due to Capt. F. van Urk of Walvis Bay for the donation of the two scorpaenids and to Mr Theo Schoeman of Windhoek for his cheerful assistance under unpleasant conditions on the Namib coast during October 1978.

The visit to the Skeleton Coast Park was made with the permission of the Director, Division of Nature Conservation and Tourism, Mr B. de la Bat, and with the assistance of Mr E. Karlova, Senior Nature Conservator of the Park. Publication is with the permission of the Secretary for National Education.

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POSTEL, E. and ROUX, C.

SMITH, M. M.
SHORT NOTE

Sight records of the Egyptian vulture from South West Africa/Namibia

by

C. F. Clinning

Nature Conservation and Tourism Division,
SWA Administration

Received: 14 November 1979

According to Mundy (1978) there are no recent records of Neophron percnopterus from South West Africa, five acceptable records for the territory all dating from before 1945. Clinning and Jensen (1979) mention an Egyptian vulture seen on the coast, north of Swakopmund, in June 1978 without giving any evidence to substantiate this record. I know of seven subsequent records from South West Africa.

This note examines these records in the light of McLachlan and Liversidge's (1978) statement that recent sight records are required and bearing in mind the pitfalls mentioned by Mundy (1978).

The immature photographed north of Swakopmund on 25th June, 1978 was seen flying in an area almost devoid of vegetation. A strong easterly wind was blowing at the time and the bird had difficulty flying against this so that at times it appeared to be in danger of being blown out to sea. When disturbed it would fly only a short distance before settling again, and was followed for some four to five kilometres, by vehicle, before it disappeared over a ridge and could not be re-located. During this time good views were obtained of the bird both settled and in flight, using 10x binoculars. Photographs taken at the time are of too poor a quality to warrant reproduction. Observations were made in the company of my wife and Dr. P. D. Shaughnessy of Cape Town. The bird was identified as an Egyptian vulture by the following combination of characters.

(i) Plumage dark brown, somewhat mottled with lighter brown on the shoulders and upper wing coverts, and also on the upper tail and rump. In flight the under-wing coverts paler than the flight feathers.

(ii) Head and neck completely feathered.

(iii) Face bare, skin pink to pale grey, lighter posteriorly, almost white where feathers replace bare skin behind the eye.

(iv) Bill yellow with a dark tip, long and slender.

(v) Legs bare, orangey-pink.

(vi) Tail relatively long, and pointed.

Sources of confusion according to Mundy (1978) include booted Hieraaetus pennatus and tawny eagles Aguilta rapax, hooded vulture Necrosyrtes monachus, palm nut vulture Gymnogyps angolensis and possibly immature gymnogene Polyboroides typus.

The two eagles can be disregarded as both have feathered legs and faces, and short dark bills. The hooded vulture has a naked head and neck and a shorter, square tail. It also lacks the yellow bill of the bird observed. It is a rare bird in SWA, recently recorded only from the north east of the territory and never in the desert. Confusion with the palm nut vulture can be ruled out as the observed bird had a slim, yellow bill, with the forehead and face entirely naked, and a relatively long pointed tail. This combination of characters, in addition to the relatively long, thin wings with no underwing barring discount confusion with the gymnogene.
What must have been a young Egyptian vulture was reported from Henties Bay by nature conservator P. Bridgeford on 10 July 1978. Bridgeford's notes and sketches made at the time clearly record the feathered head and neck, bare face, long slender light coloured bill with a dark tip, light coloured bare legs and long, pointed tail. Henties Bay is some 30 km north of where the bird previously mentioned was recorded and as only twelve days separate this and the previous observation it is likely that the same bird was involved in each case.

On 24 October 1978, P. Nel, R. Hernandes and I saw a young, brown Egyptian vulture at a feeding site at Ganab (23.05S, 15.31E) in the Namib Desert. Abattoir offal, and the carcasses of game and domestic animals were dumped at this site over a period of four months in order to attract the locally breeding lappet-faced vultures *Torgos tracheliotus* in an attempt to re-sight marked birds. The Egyptian vulture was feeding on the remains of a horse which had been dumped at the site some days previously, and had been almost entirely consumed by lappet-faced vultures. Although there were several lappet-faced vultures about at the time, none were actually feeding and good views were obtained of the Egyptian vulture as it fed. Observations were made through 10x binoculars and a 40x telescope. All identifying characters as listed for the first bird above were noted and I am confident of the identification.

On 8 and 9 February 1973 nature conservator A. van Vuuren recorded a white vulture on Andoni Plains Etosha National Park. Dr. H. Ebedes (in litt.) recalls that he and Van Vuuren discussed at length the identity of this bird and eventually decided that it was a palm nut vulture. The bird is not adequately described in Van Vuuren's original records and could have been an Egyptian vulture.

Dr. H. Ebedes (*in litt.*) recalls seeing what he identified as an Egyptian vulture at Gobabeb, Etosha National Park. Photographs indicate that this bird may have been a hooded vulture.

Godschalk (1976) records an adult Egyptian vulture flying over Ombika Gate, Etosha National Park on 20 January 1975 but gives no description to substantiate this record.

In late November or early December 1978 (exact date uncertain) a single bird identified as an adult Egyptian vulture was recorded drinking at Klippan, Otjozandu area, Otosha National Park by nature conservator C. Eyre. On 12 January 1979 Eyre recorded an adult Egyptian vulture at Khoaobendes, also in the Otjozandu area of Etosha National Park. This bird was in the company of five white-backed vultures *Gyps africanus* at an eland carcass, but stood to one side while the others were feeding.

Eyre's descriptions record only that the birds were white with darker flight feathers and that they were smaller than the white-backed vultures, with feathered, not naked, necks.

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American sealers from the schooner *Antarctic* under the command of Captain Benjamin Morrell visited most of the islands along the west coast of southern Africa between September 1828 and May 1829 to collect skins of the Cape fur seal *Arctocephalus pusillus*. Morrell's (1832) description of that journey is one of the few published accounts by early visitors to the coast of SWA. The journal of a member of Morrell's crew provides more detail of the 1828/29 cruise than Morrell's version. Portions of it have been reproduced by Best and Shaughnessy (1979), who attributed it to John Keeler and compared it with the account by Morrell.

Keeler recorded three groups of islands between Lüderitz and Possession Island, namely Shag Rock, South Rocks and Ladys Rocks. Best and Shaughnessy deduced that the first two refer to Halifax and Long Islands, respectively. Judging from the time that Keeler recorded for a return journey from Possession Island in a small sailing boat, and by the absence of other possible islets, they deduced that the Ladys Rocks group was in Abenteuer Bay.

![Figure 1: Map showing the location of Ladys Rocks.](image)

There is a group of three small islands situated at 26°51.5'S, 15°09'E in a small bay between Lüderitz and Possession Island (Fig. 1). The bay is named Abenteuer on the 1:50 000 topographic map 2615 CC published in 1976, but Bain's Bay on the South African Navy chart SAN 110 and in the South African Sailing Directions (Tripp 1975). The latter includes an aerial photograph of the islands. The northern headland of the bay is consistently known as Zweispitz. As the islands are not named in any of the aforementioned sources, and as there are no other islands in the bay, it may be inferred that it is these islands that Keeler named Ladys Rocks.
Landings were made at Lady's Rocks on 24 January 1979 from the Sea Fisheries patrol boat *Nautilus II*. They are 0.5 km from the coast of Diamond Area No. 1. The northern rock was bare except for small numbers of roosting bank cormorants (*Phalacrocorax neglectus*) and kelp gulls (*Larus dominicanus*). Although it is 6 m high, its size (10 x 5 m) appeared insufficient to prevent large waves washing over it.

The middle rock is 0.1 km south of the northern one. It is the largest (30 x 10 m), is 3 m high on the western (bare) side but is lower on the eastern side. A colony of 56 bank cormorants and one white-breasted cormorant (*P. carbo*) was nesting on a guano deposit on the eastern side of the rock. The bank cormorants were sitting on eggs and chicks; the white-breasted cormorant was guarding a single chick half its size. Kelp gulls were also nesting on the island; five chicks were found and two nests (c/2 and c/3). Forty kelp gulls, 34 Hartlaub's gulls (*L. hartlaubii*), six swift terns (*Sterna bergii*) and 20 turnstones (* Arenaria interpres*) flew off the rock as it was approached. Adjacent to the guano patch was another guano-encrusted area which was bare of birds. The presence of Hartlaub's gulls and swift terns on the rock suggests that they may have deposited the guano while nesting there in recent years. The swift terns and turnstones have been referred to by Cooper *et al* (in press).

The southern rock (8 x 4 m) supported only roosting cormorants; 42 bank, two white-breasted, two Cape (*P. capensis*) and one crowned (*P. coronatus*). The close proximity of this rock to the middle one (10 m distant) probably explains why Tripp (1975) only recognised two rocks in the bay.

A second visit to Lady's Rocks was made on 10 July 1979. Cormorants and gulls were roosting there, but none was nesting.

Despite the fact that no seals were seen on Lady's Rocks during either visit (of which the former occurred when large numbers were ashore at nearby breeding colonies), the topography of the rocks (particularly the middle one) suggests that a small colony of seals could have existed there in the past. According to Rand (1972) there are five islands off the coast of SWA where Cape fur seals formerly occurred (Mercury, Ichaboe, Seal, Penguin and Possession), but were apparently exterminated. Best and Shaughnessy (1979) added Lady's Rocks to that list (on the basis of the visit reported here), as well as Plumbudding Island.

The status of the bank cormorant is listed as uncommon and vulnerable by Siegfried *et al* (1976). As Lady's Rocks contains a small breeding colony of that species, access to them should be prohibited and the birds there protected.

**ACKNOWLEDGEMENTS**

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SIEGFRIED, W. R., FROST, P. G. H., COOPER, J. and KEMP, A. C.


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