also formed part of the prey. Porcupines provide the most significant direct secondary influence. They gnawed bones on the living area and/or removed them to their burrows (sometimes disused hyaena burrows). Striped polecat, rock kestrel and marsh owl used the area and may introduce remains of their prey to the general accumulation. Marsh owls were observed to deposit large quantities of pellets in the area.

Large numbers of hyaena scats occurred in discrete 'toilet' areas, although bones and scats were mixed in places where the significance of eating or defecating had changed over a period of occupation or with renewed occupation. Most scats consisted of hair and disintegrated rapidly as a result of the activities of clothes moths and other organisms. A few contained sufficient calcium remnants of bone to be sufficiently hard to be preserved as potential fossils. Hair-filled scats included distinctly eroded bone and teeth fragments. These supply a further characteristic input of bone to accumulations. Jackal scats are more dispersed, less often calcified, and unlikely to be preserved. Identifiable bone fragments of smaller prey are also found in them.

Prey of both species varied but even accumulations some distance inland included an important coastal component. In the case of hyaenas, remains of smaller species are under-represented as they are almost completely chewed up and do not readily survive digestive acids. Proportions of different species do, however, appear to reflect those of living populations in the area. The role of hunting is not clear. Scavenging on the beach and ungulate prey remains of lions and cheetahs were the most common means of obtaining food. Similar marine prey was taken by hyaenas and jackals but because the latter cannot break up bones as efficiently as hyaenas, clear differences exist between the damage and body-part representation after feeding by adults of the two species.

Brown hyaenas are well known accumulators of bones. Jackals, too, are important accumulators where a regular source of food attracts them consistently. The composition of jackal accumulations on the coast is very similar to those of prehistoric human hunter-fishers.

Digestive Physiology and Adaptations of the Hyrax, *Procavia capensis*, to Semi-arid Environments

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Procavia capensis is a true herbivore with an enlarged hindgut. Laboratory results of digestion studies on hyrax fed three different diets were compared with ruminants and other non-ruminants. Feeding hyrax maximize intake in a minimum time, feed twice a day and delay food in the sac when fed on a high fibre diet. Delaying transit of ingesta would decrease searching time for food, reduce exposure to predation and also enable hyrax to consume poorer quality food.

Hyrax digest lignified cell walls very well with efficiencies comparable to those of capybaras and horses. Volatile fatty acids contributed up to 58% of the basal metabolic requirements with the highest production of 33% in the sac, emphasising its fermentative importance.

During the Miocene, development of grasslands forced hyrax to leave the plains for the protection of rocky outcrops; this, coupled with environmental and body-size changes, probably led hyrax to develop hindgut fermentation as their major adaptation to a diet high in fibre content. Behavioural and other physiological adaptations such as thermoregulation and urine osmoregulation enble hyrax to penetrate arid environments.

Aspects of Thermoregulation and Water Balance in the Springbok

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In wild African ungulates, the thickness of the pelage decreases exponentially with increasing body size and springbok have a thinner than predicted pelage. The thin pelage imposes certain thermal disadvantages on this species but is of great importance for dissipating the metabolic heat generated when sprinting away from predators.

Springbok maintain a reasonably stable body temperature under a variety of climatic conditions and their adaptation to a hot dry environment can be attributed largely to their thermoregulatory behaviour and specific physical qualities of the pelage. They orientate their long body axes parallel to the sun's rays to reduce solar heat load and the pelage has a relatively low absorption of short-wave radiation. These adaptations are supported by efficient renal function.

Some Aspects of Rodent Ecology in Semi-arid Environments in Southern Africa

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The breeding habits and population dynamics of the bushveld gerbil Tatera leucogaster, the striped mouse Rhabdomys pumilio and the vlei rat Otomys irroratus have been examined in relation to rainfall and diet in semi-arid environments. R. pumilio is an unspecialized omnivore exploiting transient but nutritious foods, which may account for the seasonality of its breeding and its fluctuation in density. O. irroratus is a specialized herbivore that utilizes constant and abundant, but relatively poor quality, foods to maintain year-round breeding and a stable population. The iteroparity of O. irroratus may have co-evolved with adaptations to herbivory to exploit abundant but low protein food resources. T. leucogaster is a selective feeder on ephemeral but seasonally available insects and seeds, but feeds on herbage when preferred foods are unavailable. Breeding is seasonal and associated with regular summer rainfall, however, the duration of the breeding season is variable. Litter size is large and the semelparity of T. leucogaster is associated with an extreme xeric environment.

Method of Censusing and the Status of the Black Rhinoceros (*Diceros bicornis*) in the Etosha National Park

1218

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During the periods of full moon from May to October 1980, black rhinoceroses were censused at all the important waterholes in the Etosha National Park. Identification based on anatomical features (particularly horns and notches in ears), group composition and behaviour, revealed a population of at least 350 rhinoceroses of which 45 – 50% occurred in the west of the park. This technique is effective in areas where rhinoceroses need to drink at established water-points and it was shown to be up to 70% more accurate than census by helicopter. In addition, information is obtained on behaviour, inter- and intraspecific relationships and population dynamics.

The results indicate an increase in the rhinoceros population which was substantially higher than expected. However, the high population in the west, where in some areas apparent over-utilization of the available food resource was evident, has since been affected by drought, anthrax and in particular poaching. From 1981 to June 1983, 17 mortalities relating mainly to unnatural causes were recorded, including 7 confirmed cases of poaching. As a consequence, in certain areas, many rhinoceroses have left traditional home ranges and a number of unrecorded mortalities are suspected. Control measures include the successful translocation of 29 rhinoceroses to the east of Etosha and in 1981, the vaccination of 36 rhinoceroses against anthrax.

With anti-poaching measures presently being inadequate, poaching poses the greatest threat to the black rhinoceros population. The implementation of effective anti-poaching measures has become a matter of urgency and is presently receiving attention.

Marking Technique for the Identification of the Black Rhinoceros (*Diceros bicornis*) in Arid and Semi-arid Ecosystems

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Colour-coded reflector discs 20 mm in diameter and 3.5 mm thick, were inserted at the base of the anterior aspect of the front and the lateral sides of back horns of adult and sub-adult rhinoceroses, to facilitate the positive identification of translocated animals. Disc components comprised reflective tape, with printing plate at the back and transparent polycarbonate on the surface. Three colours, red, green and yellow, were used. With the aid of a torch, spotlight and binoculars, marked rhinoceroses were identified at night when they came to waterholes to drink. Because of horn wear, reflectors are temporary and function for approximately 6 months when affixed with epoxy resin 0.5-1.0 cm below the horn surface. Ear tags were unsatisfactory and mostly tore out, but are nevertheless recommended, particularly for marking calves and juveniles.

Using reflectors, it was possible to plot the resettlement of 9 out of 10

rhinoceroses introduced to new surroundings in the Etosha National Park. The technique is recommended when monitoring and resettling rhinoceroses in arid and semi-arid environments, where they are required to drink at established water-points.

Biogeography and Ecology of Waterbirds in Arid Sub-Saharan Africa

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Both uni- and multi-variate statistical approaches were employed in analyses of waterbird distribution maps in the Atlases of Speciation of African Birds [Hall & Moreau 1970 and Snow 1978, British Museum (Natural History)].

Two major arid zones were identified, one in the north-east, the other in the south-west of Africa. The boundaries of these zones are delineated by the range limits of species which cannot exploit the severe, highly variable and unpredictable desert environment. Not unexpectedly, species richness and endemism are low in these arid areas. However, the decline in species richness is not as steep for waterbirds as for non-aquatic birds as one progresses from a mesic to a xeric environment.

Within these arid zones there is an over-representation of large, mobile birds which prefer discrete water habitats (e.g. pond, vleis, etc.). These morpho-ecological attributes allow the exploitation of highly geographically and temporally variable habitat and food resources which characterize these zones.

A comparison of the north-east and south-west arid zones reveal some interesting differences. The north-east arid zone has an over-representation of waterbirds which are regular intra-African migrants, and the south-western zone an over-representation of ducks and birds which undertake irregular, opportunistic movements, and use swimming (as opposed to wading) as their primary means of locomotion while foraging. This may reflect a relatively more predictable environment in the north-east arid

Arid-zone Adaptations of Waders (Aves: Charadrii)

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Both major lines of wader evolution have produced arid-adapted forms, the seedsnipe (Thinocoridae) from the scolopacoid line, and the coursers (Glareolidae, Cursoriinae) from the charadrioid line. Both lines derived from a common ancestor that probably inhabited marine shores for which basic adaptations were (a) long legs for wading, (b) short toes for running on hard substrates, or long toes for support on soft mud, (c) paired supraorbital glands for secreting excess NaCl taken in with seawater or invertebrate food, (d) cryptic plumage for shoreline nesting, (e) a small clutch of cryptically coloured eggs to be laid in an exposed site. In addition, certain basic avian adaptations included high tolerance to insolation, and a generalized diet of invertebrates and some plant material.

All these features constitute pre-adaptations to arid zones. They have been retained almost unchanged in plovers (Charadriidae) and coursers. Two predominantly seed-eating groups, the seedsnipe of South America and the sandgrouse (Pteroclidiformes, Pteroclididae) of Africa and Asia, have developed short legs; sandgrouse, at least, have also lost the salt gland in response to drinking relatively large amounts of water. Evidence shows that sandgrouse can be derived from the same basic line that gave rise to the coursers. Soaking of the belly feathers in many tropical charadriiforms on the charadrioid and laroid (gull) lines has become highly evolved in sandgrouse as a method of transporting water to their young.

Diet of Helmeted Guineafowl in a Semi-arid Environment

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The oven-dried crop contents of 218 helmeted guineafowl (Numida meleagris) shot near Kimberley during years with high and low rainfall were analysed quantitatively by mass. Vegetable food, especially underground storage organs of sedges of the family Cyperaceae, predominated in nearly all crops. The mean total mass of crop contents of birds shot during the non-breeding season (winter) of a high rainfall year was greater, and had a

relatively higher percentage of animal food, than that of birds shot during the winter of a low rainfall year. There was no significant sexual variation in diet among non-breeding birds.

However, combined data from two breeding seasons (summer) indicate that female quineafowl consumed more food than their mates and took a relatively higher percentage of animal food. This is due to the fact that breeding females spend a much higher percentage of their time feeding than their mates, which spend much of their time in alert postures, chasing or fighting with other males, or in courtship-feeding of their mates. Also, animal food (mainly grasshoppers, beetles, ants and other invertebrates) is most abundant during this time.

In the non-breeding season adult guineafowl consumed more food than juvenile birds, but the latter took a higher percentage of animal food than the former. Birds shot in the afternoon had eaten more than birds shot in the morning.

The first result is probably due to an age-based dominance of adults over juveniles, especially over defensible food resources such as the underground storage organs of plants. The higher percentage of animal food in the crops of juvenile birds could be a consequence of their preference for high protein food necessary for continued growth, or a 'second-best' choice of an undefendable food resource.

Adaptiveness of Nest Site Placement in the White-browed Sparrow-weaver *Plocepasser mahali*

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Observations on 4546 white-browed sparrow-weaver nests in the south-western Transvaal and in the northern Cape indicate that sparrow-weavers build their nests on the south side of nest trees. Environmental parameters were measured for nests, nest trees and colonies that occupied more than one nest tree. Temperature and humidity measurements in and around breeding nests indicate that solar radiation and humidity are not important factors in the choice of nest sites by sparrow-weavers. Wind measurements from weather stations at the present and close to the areas of four other survey sites of sparrow-weaver nests¹⁻⁴ were compared to the nest site orientation at the respective sites. Nest site orientation was not correlated with the direction from which strong winds blew. Nest site orientation was also not influenced by the shelter afforded by either the leaf density of the nest tree or the presence of nearby trees. In all cases, nests were situated on the side of trees opposite to the prevailing wind.

The observed nest orientation is seen as an adaptation to reduce wind-induced erosion on sparrow-weaver nests. Predation on sparrow-weavers appears to be high^{5.6} (recruitment rate = 11% during present study) and would be enhanced because the semi-arid areas offer only dry grass stems with which the birds build conspicuous nests. During the present study, each sparrow-weaver had on average eleven roost nests. The observed nest site orientation is postulated to aid in the maintenance of a high number of nests per sparrow-weaver, which in turn is an adaptation against predation on sparrow-weavers that occupy breeding or roost nests.

The characteristics of a semi-arid environment — dry grass stems, good visibility experienced by predators, wind and cold nocturnal temperatures — are postulated to combine in causing sparrow-weavers to maintain a high number of roost nests per bird.

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Breeding of Two Passerines after High Rainfall in the Skeleton Coast Park

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Above average rains fell throughout the Skeleton Coast Park and neighbouring areas during March/April 1982: rainfall was measured at Möwe Bay (31.9 mm), Ugabmond (26.3 mm) and at Springbokwater (60 mm). Owing to the increase of vegetation and the abundance of insect life, many birds invaded these areas and bred. The most prolific breeding species