Maclean, G.L.
1990.
Ornithology for Africa
University of Natal Press
Pietermaritzburg.
P110

Adaptations to pollination by birds also include robust floral structures, stems, spathes or leaf clusters for the birds to perch on while extracting nectar. The average length of the corolla tube matches very broadly the bill lengths of the principal pollinators: *Erica* has a mean tube length of 19,3 mm and *Aloe* of 40,1 mm (Rebelo 1987b). The Orangebreasted Sunbird, an *Erica* specialist, has a bill of 20–23 mm in length (Maclean 1985b). Although the bill lengths of the other sunbird species of the Cape Flora vary from 13–34 mm in length (Maclean 1985b), they are still able to extract nectar from *Aloe* flowers because the floral parts are unfused and can be spread apart by the birds' heads, allowing them to penetrate to the base.

The Cape Sugarbird is a *Protea* specialist with a bill measuring 30–36 mm in length (Maclean 1985b). *Protea* (Plate 8e) and *Leucospermum* (both Proteaceae) have 'brush-type' flowers whose anthers and styles form the external surface of the pollination unit, protruding 10–36 mm above the nectar source (Rebelo 1987b), though these flowers may also be visited by insects.

Ornithophilous plants of the fynbos occur almost exclusively on soils poor in nitrogen, phosphate and potassium, which means that the plants can produce few seeds, but much carbon-rich tissue such as wood and nectar. Water is not a limiting factor, since these plants flower during the rains, so a lot of dilute nectar can be produced economically (Rebelo 1987b).

The fynbos grades gradually into the semi-arid regions of the Karoo to the east and northeast. As I have mentioned, the two vegetation types share both plants and animals, though the arid-zone adaptations of the organisms are perhaps more finely tuned and better adapted to a largely summer-rainfall region.

9. Arid and semi-arid habitats

9.1. Causes of aridity

Aridity is the result of more or less permanent high-pressure zones that form over the tropics north and south of the equator (Figure 5.7). Air heated at the equator rises. As it does so, it cools and releases much of its moisture in the form of rain. Once cooled it begins to descend again, warming up in the process and becoming relatively drier: this is to say that its *relative humidity* decreases. As the moisture content gets lower and lower, there is less and less screening of the sun's rays through the very dry air, and the effects of sunlight (insolation) are greatly exaggerated, leading to increased heating of and radiation from the land. Because of the dry conditions, vegetation is sparse, allowing the sunlight to strike bare ground. The combined effects of reflection and radiation increase the aridifying effects of the dry air and the direct insolation.

According to Shmida (1985) the average annual rainfall in a semidesert is 150–400 mm, in a 'true desert' 70–120 mm and in 'extreme desert' less than 70 mm. For purposes of this account I have classed semidesert as a region with an average annual rainfall of 125–250 mm (such as the Karoo, Kalahari and Sahel) and desert as having less than 150 mm a year

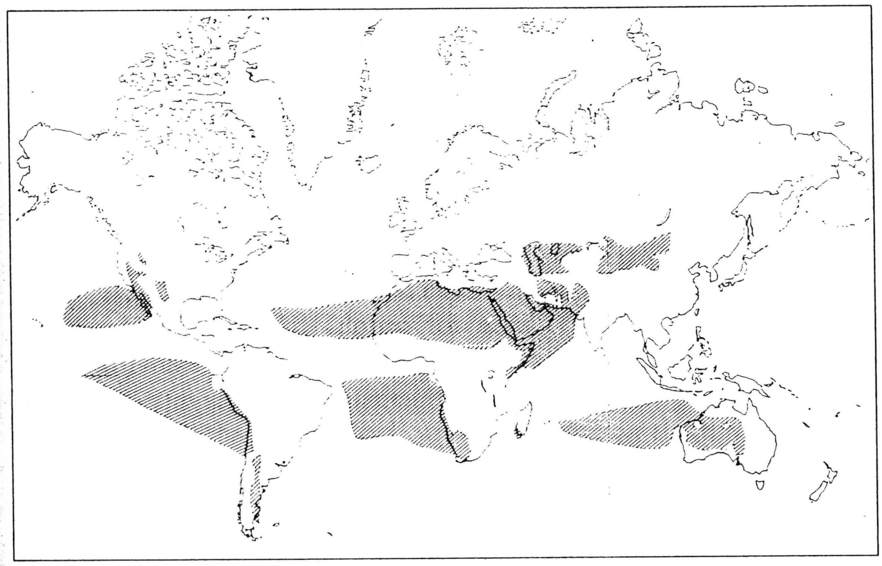


Figure 5.7
The high-pressure systems of the world; the affected land surfaces are arid to semi-arid (adapted from Logan (1968)).

(such as the Namib, much of Somalia and the central Sahara). The arid regions of the world are characterized by plants of the families Chenopodiaceae, Zygophyllaceae (the only two families actually centred on arid zones worldwide) and Aizoaceae (centred in the deserts of southern Africa). Among desert trees the genus *Acacia* is one of the most characteristic. The only plant endemic to true desert is *Welwitschia mirabilis* of the monotypic family Welwitschiaceae confined to the Namib Desert (Shmida 1985).

The Karoo, a semi-arid shrubland (Plate 8f), grades naturally from the grasslands of the South African highveld in the east and merges in the west with the Namib and the fynbos, and in the north with the southern Kalahari (Plate 8g). The Karoo is a large summer-rainfall area on an inland plateau mostly south of the Orange River (Werger 1986). The Kalahari is a semidesert only in its southern and western parts, but is a waterless region or 'thirstland' because its sandy nature does not allow surface water to accumulate and lie for any length of time. Over most of its area the Kalahari is a dry *Acacia* savannah in which the Camelthorn *A. erioloba*, the Grey Camelthorn *A. haematoxylon* and the Hookthorn Acacia *A. mellifera* var. *detinens* predominate.

The Namib (Plate 8h, i) is largely a fog desert extending about 2 000 km from the Olifants River in Namaqualand to Mossamedes or the Rio San Nicolai in Angola and varying in width from 80–150 km. It is partly sandy (Plate 8h) and partly stony or gravelly (Plate 8i). It is caused by a permanent temperature inversion formed by a layer of cold air overlying the Benguela Current up to a depth of 600 metres, which blocks warm easterly air (Walter 1986). The rainfall is about 9–27 mm a year, but an almost permanent fog bank over the sea (whose surface temperature averages about 12°C) rolls inland on most nights of the year to provide condensed moisture for plants and animals. The region south of the Orange River receives winter rain and resembles the Karoo. North of the Orange the scanty rain falls mainly in summer, ranging from 50–100 mm in the Inner Namib to infrequent episodic rain in the Outer and Coastal Namib regions (Walter 1986). Overall the Namib receives less than 10 mm of rain in 50% of the years during which records have been kept (Van Zinderen Bakker 1975). The arid conditions of the Namib date back to about the early Oligocene; it is taxonomically one of the richest deserts in the world, whose high degree of endemism among its living organisms attests to the desert's great age (Van Zinderen Bakker 1975).

The arid zones of southern Africa are increasing in size, especially around the margins of the Karoo, as a result of overstocking and general land mismanagement – a cause for serious concern. The birdlife is characterized by a high degree of endemism and the environmental conditions by rather unpredictable fluctuations of droughts, floods and outbreaks of the Brown Locust.

The ecology of arid-zone birds in Africa has been well studied and reviewed (Maclean 1974, 1976a, 1984a, b, 1985a, and references therein). The account that follows is drawn largely from these publications, augmented where necessary by the works of others. The Somali deserts have been poorly covered ecologically and are much younger in age than, for example, the Namib (Van Zinderen Bakker 1975). Much the same can be said of the more arid parts of the Sahel. The Sahara is largely Palaearctic and forms part of the Great Palaearctic Desert extending from the Atlantic Ocean to China (Casselton 1984).

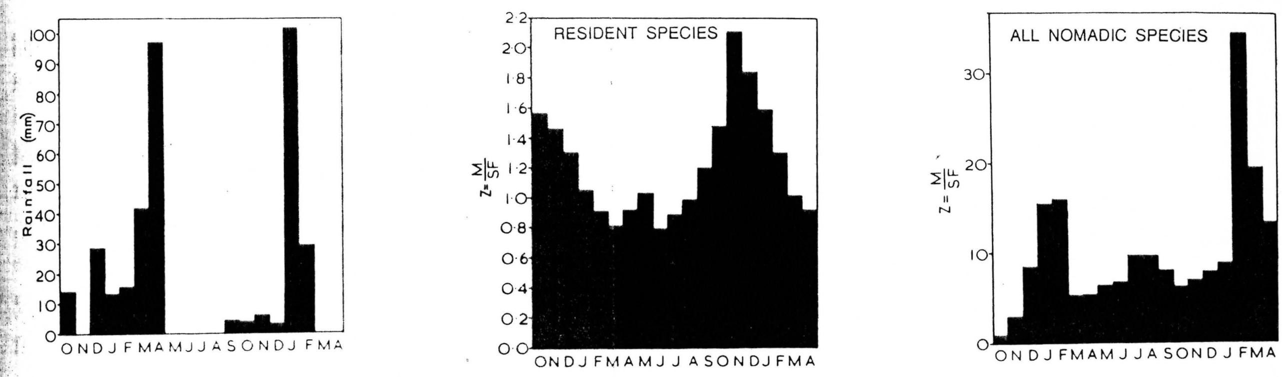
9.2. Water

The main problems confronting birds of desert regions are a scarcity of water, cover and shade, erratic food supplies which may be locally but temporarily abundant, intense insolation resulting in great heat by day, and clear skies acting as a heat sink at night resulting in low night-time temperatures. The general scarcity of water is perhaps the greatest single problem facing any arid-zone organism, since it is aggravated by high daytime temperatures; this problem is especially acute for animals, since evaporative cooling uses precious water. Birds get their water in three ways: (a) by drinking, (b) as 'preformed' in their food, whether plant or animal and (c) from their own metabolic processes.

Drinking water is by definition limited and widely scattered, and is often too brackish or saline to be of any use to birds. Nevertheless a surprising number of desert birds are obligate drinkers and must fly to a waterhole daily or at least, in the case of sandgrouse, every second or third day or even every fifth day (Thomas & Maclean 1981). The frequency of

Table 5.7 An analysis of the diet of five species of Namib Desert larks, all of which are independent of drinking water (data from Willoughby (1971)).

Species	Percentage of food in diet		
	Seeds	Insects	Green plant
Karoo Lark *Mirafra albescens*	32	68	trace
Spikeheeled Lark *Chersomanes albofasciata*	16	84	trace
Gray's Lark *Ammomanes grayi*	56	43	1
Stark's Lark *Alauda starki*	77	19	4
Greybacked Finchlark *Eremopterix verticalis*	91	8	1



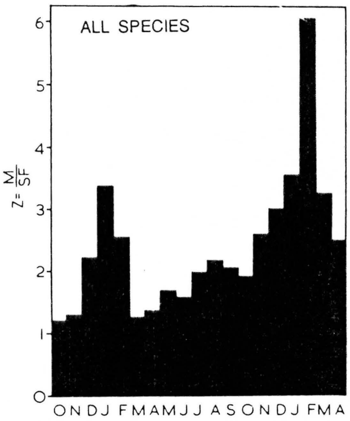


Figure 5.8
The effects of rainfall on populations of birds in the Kalahari Gemsbok National Park in the semi-arid Kalahari sandveld, showing the influence of nomadic species on numbers. The formula Z = ΣM/SF *is an index of population size per month, where* ΣM *is the monthly total for a species or category,* F *is the number of field trips for that month and* S *is the number of species per category of occurrence for that month (i.e. resident, nomadic,etc.) (from Maclean 1970b).*

drinking increases in summer when the birds are using water for evaporative cooling by panting or by a process called gular-flutter whereby the floor of the mouth and the throat are rapidly pulsated in order to pass air quickly over these moist surfaces to facilitate evaporation. Seedeating birds, such as doves, sandgrouse, sparrows and waxbills, need to drink greater amounts of water more often than do most insectivorous or frugivorous birds, since seeds contain little moisture – sometimes as little as 15%.

The resistance of desert birds to dehydration is remarkable: the Namaqua Sandgrouse and the Blackthroated Canary can survive without water for at least 14 days under moderate temperature conditions, though they lose weight steadily. The Redheaded Finch, Cape Sparrow and Larklike Bunting, all regular drinkers in the wild, can survive indefinitely without water on a diet of air-dried seeds only (Willoughby & Cade 1967). An especially well adapted species is the Scalyfeathered Finch which can even gain weight on a diet of dry seed and no drinking water at all (Cade 1965). Even a small proportion of insect or succulent-plant food in a bird's diet can make it completely independent of drinking water (Table 5.7) (Willoughby 1971).

Insectivorous birds usually get enough water from their food to obviate the need to drink. However, the body fluids of their prey may contain enough salts to require their extraction by the kidneys or some other mechanism as a water-conservation measure. Most birds appear to be able to get by on their kidney physiology alone (the kidneys of desert birds are better at dealing with hyperosmotic solutions than those of birds of non-desert habitats), but some charadriiforms, such as the Doublebanded Courser and the Crowned Plover certainly use their supraorbital salt glands for excreting hypersaline solutions via the nostrils. A study in the arid zone of inland Australia showed a parallel case in the Australian Dotterel, which has well developed salt glands of the type found in marine birds (Plate 9a) (Maclean 1976b). Seawater has an osmotic concentration of about 1 000 milliosmoles per litre (mOsm/litre), while most avian blood contains about 370–400 mOsm/litre. Salt glands are capable of excreting solutions of up to 2 000 mOsm/litre and, in the case of the Gabar Goshawk, as much as 4 950 mOsm/litre, so the mechanism is a highly efficient one.

Even so, many desert birds have to function without any salt gland at all: the passerines and the sandgrouse are examples. They avoid hyperosmotic drinking water when possible, but the Namaqua Sandgrouse and Burchell's Sandgrouse can survive on water with a concentration of up to 430 mOsm/litre.

Because seeds tend to be concentrated in time and space, most granivorous birds of arid regions are both nomadic and gregarious. Most insectivorous birds in arid regions are solitary and fairly sedentary, indicating a low but fairly constant food supply. The movements of the nomads are governed almost entirely by rainfall (Figure 5.8).

9.3. Thermoregulation

Most desert birds are diurnal. Activity generates heat in a bird's body, so that birds tend to be more active in the cooler morning and evening hours than at midday when ambient temperatures may exceed 40° C in summer. Birds employ various techniques in order to avoid excessive buildup of heat by day. The two most obvious are to remain inactive and to seek shade, usually of bushes, trees or rocks. The surface area of the body through which heat may be lost by conduction and radiation may be increased by drooping the wings, spreading the wrists away from the body and standing high on the legs (Plate 9b). In order to reduce insulation the plumage is sleeked to eliminate air, and all uninsulated body parts (bill and legs in particular) are fully exposed and shaded to act as 'thermal windows' through which heat is dissipated.

Where shade in the form of plants or sizeable stones is scarce or absent, birds such as Gray's Lark will perch above ground level on stones or twigs where the temperature is a few degrees lower than on the desert floor; by facing into the wind they are able to increase their heat loss by conduction. Another strategy, used by the Spikeheeled Lark is to shelter from the sun in rodent burrows. A special case is that of the Sociable Weaver, whose huge nests (Plate 9e) provide shade by day and shelter from the cold on winter nights.

Physiological heat-loss mechanisms include panting and gular-flutter which enhance the evaporation of moisture from the respiratory system and buccal cavity. Evaporation is a widely used cooling mechanism among endothermic animals, but it is not generally known that birds evaporate water through the skin as well as from the internal mucosa. Marder, Gavrieli-Levin & Raber (1986) showed how Spotted Sandgrouse, a Saharan species, did not always gular-flutter when heat-stressed and that the temperature of the skin was always lower than that of the body, indicating cooling by evaporation through the skin; the

Table 5.8 Mean body and skin temperatures of six Spotted Sandgrouse measured at different high ambient temperatures (°C) under experimental conditions, showing the cooling effects of cutaneous evaporation (Marder, Gavrieli-Levin & Raber 1986).

Ambient temperature	Body temperature	Skin temperature
27	41,4	40,3
42	42,0	41,3
45	42,4	41,6
51	42,6	42,1

body temperature was kept to around 42,5°C, even at ambient temperatures of more than 50°C (Table 5.8). The same sort of temperature control has been shown in southern African sandgrouse species (Thomas & Maclean 1981).

9.4. Camouflage

Since most arid-zone birds live on the ground, they need to be protected from predation by cryptically coloured plumage. Resident or sedentary birds generally match their backgrounds very closely; where they have widespread populations, these can be divided into local races that vary in colour according to the colour of the soil or rock on which they live (Plate 9c). Nomadic species are cryptic in a less closely matching way, since they have to be inconspicuous on a variety of rather different backgrounds. One can therefore distinguish between 'specialized cryptic' and 'generalized cryptic' kinds of birds, but the overall principle in camouflage is to have dull colours and appropriate behaviour (usually an instinctive tendency to crouch motionless on the ground when threatened).

9.5. Breeding adaptations

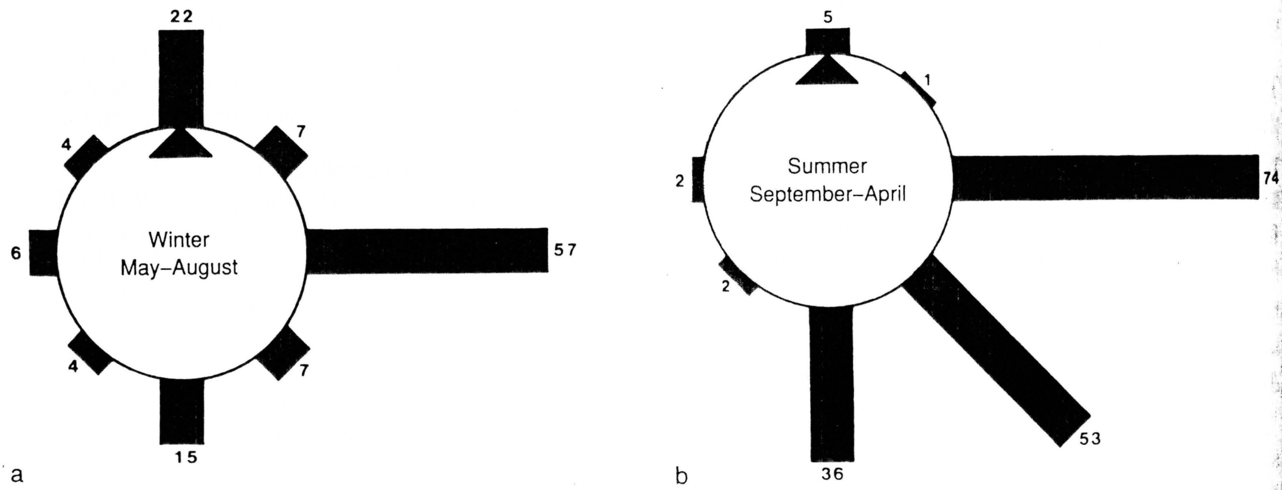
The arid environment presents special problems to birds with regard to the timing of breeding. (This topic is more fully covered in Chapter 8, to which reference can be made.) The main criterion governing this is the availability of food, not only for the adults to initiate breeding and for the female to lay eggs, but also for feeding the young when they have hatched. Since these are related to other matters pertaining to breeding, they will largely be treated under that general heading in Chapter 8. In this section I shall outline only a few of the adaptations of certain Afrotropical desert birds in their pursuit of reproduction.

One of the most exciting and remarkable of these adaptations is that of sandgrouse to carrying water in their belly plumage for the purpose of watering their chicks (Cade & Maclean 1967). This behaviour is better developed in the males than in the females, possibly to allow the females to retain dry plumage for brooding the young at low ambient temperatures. This has been best studied in the Namaqua Sandgrouse: the male soaks his belly feathers during his morning drink (Plate 9d), flies to where the chicks have been left crouching (with or without the female's protection) and presents himself to them in an upright posture which signals that they should come and take the water from the wet plumage. The belly feathers are specially adapted to taking up water and holding it during the male's flight from the water, a distance of perhaps several kilometres.

Another adaptation which enhances breeding success in the arid zone is the large, permanent nest structure of the Sociable Weaver (Plate 9e). Though probably evolved mainly as a protected roosting place, the permanence of these nest masses allows the weavers to start breeding immediately after rain initiates suitable conditions, since they have no need to build a nest before egg-laying. This allows the Sociable Weaver to start egg-laying as early as six days after the first good rains of a season – by far the shortest lag period known for any desert bird.

Finally the orientation of the nests of ground-nesting birds may be mentioned here, particularly with regard to protection from the sun. The best example of this is that of the larks: breeding may take place at any time of the year, depending on the timing of the rains, so that nests may be found in midsummer as well as in midwinter. Summer nests are invariably placed under the shelter of a plant or stone, and are orientated significantly frequently to the east, southeast and south of the sheltering object (Figure 5.9a); this is the shadiest sector of the compass, since in the southern hemisphere the sun passes to the north. In winter when the sun is less fierce and poses no threat to birds in the open, the orientation of lark nests is less clearly east-to-southeast (Figure 5.9b) and many nests are built quite exposed. The advantage of this is that such nests are less easily discovered by predators which have learned that most nests are to be found at the bases of shrubs and grasstufts. Even so, in one study the overall success rate of lark nests in the Kalahari sandveld was only 17,9%, expressed as the number of chicks that left the nest (92) relative to the number of eggs laid (513) (Maclean 1970a).

Figure 5.9
The orientation of lark nests relative to the base of a shrub or grasstuft during:
(a) a summer breeding season
(b) a winter breeding season.



9.6. Moult

Since moulting, or the replacement of worn plumage by new feathers, is a process which requires a large input of energy and materials, especially protein, arid-zone birds may have to delay their moult until conditions are favourable. An alternative strategy is to slow moult down to the point at which it is not especially demanding at any time of the year, arresting it perhaps when the birds are breeding, so that two energy-consuming processes do not usually run simultaneously. Retarded moult is found in the Chestnutbellied Sandgrouse and the Blackfaced Sandgrouse of East Africa (Kalchreuter 1979). Each wing feather or remex (the primaries on the hand and the secondaries on the forearm; Figure 2.13) is lost and regrown completely before the loss of the next one in the sequence, so that the whole process of remex moult may take as long as six months.

This may be an adaptation to maintaining a high degree of flying ability to enable these birds to fly to and from water as frequently as they do.

Another case of retarded moult is found in the Sociable Weaver (Maclean 1973). Each remex takes about a month for complete replacement, so that primary moult alone takes as much as nine months. Body moult, which takes only a month or so, occurs after rain during breeding, which is an unusual phenomenon among birds in general.

10. Montane habitats

Many ecological, floral and faunal aspects of the afromontane or afroalpine habitats parallel closely those of the fynbos or mediterranean-type habitats in Africa, though climatically the afromontane habitats have their own set of rigours with which the birds have to cope. A most readable account of the plant ecology of East African alpine habitats is that of Hedberg (1964); although there is not much on animal life, it gives a fascinating and beautifully illustrated account of the adaptations of plants to a wet but extreme climate at high elevations. High mountains are characterized by low night-time temperatures and cold winters. Little detailed work has been done on the birds of these habitats.

The observations by Coe (1967) on Mount Kenya show that there are few species of birds resident at great heights. The only two regular insectivores, the Redtufted Malachite Sunbird and the Hill Chat, feed on the sedentary insects among the leaves of the giant *Senecio* and *Lobelia* plants at 3 000–4 500 metres. The sunbird also takes chironomid larvae (a group of small flies) from tiny pools of water in the lobelia's compact rosettes of leaves. The only other fairly plentiful species is the Streaky Seedeater which is entirely vegetarian.

One of the very few studies of afromontane birds in recent years is that of Dowsett-Lemaire (1989) who concentrated on six species of sunbirds on the Nyika Plateau on the Malawi-Zambia border at an elevation of 2 100–2 200 m above sea level. Twenty-seven species of forest plants and 13 species of non-forest plants provided nectar for six species of sunbirds of the genus *Nectarinia*: Eastern Doublecollared, Greater Doublecollared, Redtufted Malachite, Malachite, Greenheaded and Bronze. Of the 40 species of flowers, 16 are insect-pollinated, 17 bird-pollinated and seven pollinated by either agent. Flowers pollinated by insects are white, blue, purple or yellow and mostly open or short-tubed. Those pollinated by birds are mostly orange, red, pink or greenish, tubular and odourless. The longer-billed species of sunbird (Bronze, Malachite, Redtufted Malachite and Eastern Doublecollared) are more efficient pollinators than the others, but there is much overlap in foraging by all the species. It appears that competition is partly avoided by habitat segregation. The parallels with the bird-plant ecology of the fynbos are obvious from this study.

A survey of birdlife in a montane habitat in southern Africa was done by Brown & Barnes (1984) in the Natal Alpine Belt of the Drakensberg. Killick (1963) distinguishes between Montane, Subalpine and Alpine Belts in the Drakensberg (Plate 9f), these being respectively at elevations