# MICROCLIMATE AND ANIMAL LIFE IN THE EQUATORIAL MOUNTAINS

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## INTRODUCTION

Eastern and central Africa possess a number of high mountains that rise above their surrounding lowlands to regions, many of which support permanent glaciers. The higher of these land masses rise to over 12,000 feet, reaching a maximum on Kibo, the main peak of Kilimanjaro which rises to 19,340 feet above sea level. This wide range of altitude is responsible for a considerable variety of climates which in turn have produced vertical stratification of vegetation types. The more easterly mountains such as Kilimanjaro, Mount Kenya, Aberdare and Elgon are surrounded for the most part by semi arid savanna, a factor which produces a more considerable degree of isolation than is found on Ruwenzori where the montane forest clothing its slopes gives way at its base to rain forest which has acted as a reservoir for many montane species.

Information regarding the microclimate of the East African high mountains is fragmentary and it is only Mount Kenya that can provide us with any real detail (Hedberg 1963, 1964; Coe 1967). Much of the information presented in this paper has been accumulated by the author and in particular the University College, Nairobi Zoology Department Expedition to the northern slopes of Mount Kenya in March, 1966.

The point where the montane forest zone gives way to the moorland and alpine zones falls between an altitude of 10,000 and 11,000 feet (3,049-3,354 m.) depending on the aspect being considered. It is these moorland and alpine areas that will be the main subject of this paper for it is here that animals at ground level are most susceptible to the alpine climate.

## MICROCLIMATE

Unlike mountains in higher latitudes those on or near the equator do not exhibit marked seasonal phenomena. Instead they possess a remarkable diurnal temperature regime through which regions above the tree line are subjected to intense heat during the day and sub-zero temperatures at night. Hedberg (1957) called this type of climate "winter every night and summer every day". This apparent state of constancy, with an even diurnal temperature range and little annual variation has produced a vegetation that is essentially slow growing but which shows little sign of seasonal reproductive activity. In turn this state is reflected in the animal life which also shows little sign of seasonal breeding.

### RAINFALL

The long and short rainy seasons of the lowlands which last from March to May and mid October to mid December are also reflected in the rainfall figures available for Mount

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Kenya and Kilimanjaro. Hedberg (1964) analysed rainfall data for the equatorial mountains and concluded that the amount of precipitation was more variable at high than low altitude and that although rainfall roughly followed the lowland pattern it was likely to be distributed over a longer period. Obtaining rainfall figures for stations at high altitude is unfortunately very inaccurate for the instruments employed are unsuitable for measuring snow, hail and the considerable addition of moisture from mist and dew.

Figures provided by Salt (1951) and Hedberg (1964) for Kilimanjaro show a marked decrease in precipitation with altitude, varying from 68·86 inches at 7,200 feet to 0·10 inches at 19,000 feet on the eastern aspect, and 48·92 inches at 9,550 feet to 0·29 at 15,350 feet on the west. Hedberg (1964) using a wider series of figures for the years 1946-1958 shows a similar decrease up to 4,500 m. (14,760) but above this altitude there is a slight increase at levels over 16,000 feet (4,878 m.).

Relevant figures for Mount Kenya also show a similar decrease with altitude but no rise at high altitude. One can perhaps best conclude that on average Mount Kenya is wetter than Kilimanjaro and that the precipitation is more evenly distributed throughout the year (Coe 1964, 1967; Hedberg 1964). The rainfall figures referred to above are all derived from rain gauges placed on the mountain's western aspect so that they do not give an overall picture of rainfall over the whole mountain.

The Kenya Government Department of Hydrology have maintained a very complete series of rain gauges on Mount Kenya since 1958 and these figures provide a much clearer idea of total precipitation and its distribution on different aspects of the mountain's surface. The east and southern quadrant may receive 90 or more inches, the west 60 inches and the north seldom more than 40 inches. The distribution of Isohyets plotted from these figures can be directly related to the depth of vegetation belts around the mountain (Coe 1964).

Little information is available for high levels on Mount Elgon which is a pity since it appears likely that this mountain may have been a radiating point for some elements of the afro-alpine flora.

Ruwenzori which lies on the Uganda-Congo border is the only mountain of the main East African group that is not volcanic in origin, and is by far the wettest, being for a large part of the year shrouded in mist. Scaetta (1934) estimated that the higher parts of this mountain received up to 64 inches per annum.

We may say that as far as animal life above the tree line is concerned rainfall probably has little direct effect upon them, though in fairly continuous periods of inclement weather the indirect effect of lowering the temperature is probably considerable, both on the invertebrate and vertebrates fauna.

### Humidity

The relative humidity in these regions fluctuates with temperature and cloud cover. In periods of damp cloudy weather on Mount Kenya the relative humidity of the air 26 cms. above ground level varied between 58 and 71%, while in bright unobscured sunlight these readings fell as low as 20%. The most remarkable feature of these changes is the speed with which the humidity can change in periods of uncertain weather (Coe 1967). This information closely follows that quoted by Hedberg (1964) for Kilimanjaro though there was no indication that the humidity fell as low as that recorded by the author.

The most recent detailed measurements of relative humidity have been made by Platt (1966) while working on the Lewis glacier on Mount Kenya. His recording station was at standard height over the Lewis glacier at an altitude of 4,750 m. (15,833 ft) so his figures cannot unfortunately be related to vegetation cover but they do none the less provide a useful indication of the diurnal cycle. His figures of mean daily relative humidity show an amplitude from 58-84% over 13 days. The mean hourly figures indicate a drop from 02·00 to 10·00 hours and a rise from 10·00 to 02·00 hours. The amplitude of these hourly measurements varies from 62-80%.

TEMPERATURE

The diurnal nature of temperature change in the equatorial mountains is the most dominant feature affecting their macroclimate. This apparent constancy of daily conditions means that although no figures are available that can be used to calculate annual means, short term means can give a fairly accurate picture of what this mean is likely to be.

The International Standard Atmosphere has a lapse rate of 2·1°C or 3·78°C per 1,000 feet (6·5°C or 11·5°F per km.), from which we can calculate the expected depression in mean temperature with altitude. These figures are only accurate within certain limits and they may not only vary in different parts of the world but also on different aspects of the same mountain (Mani 1962; Coe 1967).

Hedberg (1964) calculates that the annual isotherm for 0°C will fall somewhere between 4,500-5,000 m. on Kilimanjaro. On Mount Kenya frost will be expected on every night of the year at this altitude. Platt (1966) has shown that the air temperature above Nairobi at an altitude of 4,880 m. fluctuates annually between −0·5 and −2·0°C.

Comparable altitude figures are available for Mount Kenya and Kilimanjaro. Klute (1920) working on the Machame escarpment between August 19th and October 12th, 1912, at an altitude of 4,135 m. (13,563 ft) recorded a mean maximum of 5·17°C, a mean minimum of −0·77°C, and a mean range of 10°C. The lowest temperature recorded was −4·0°C. Coe (1967) obtained similar data during the IGY Mount Kenya Expedition in December, 1957-January, 1958, at an altitude of 4,191 m. (13,716 ft) in the Teleki Valley. These showed a mean maximum of +5·4°C, a mean minimum of −3·6°C and a mean range of 8·9°C. The lowest temperature recorded over this period was −6·7°C. There is a reasonable measure of agreement between the two sites. The lower minimum figure recorded on Mount Kenya may be attributed to the close proximity of the recording site to the glaciers.

Hedberg (1964) has calculated that the mean diurnal temperature amplitude for both the western group and the eastern group of mountains show that on average there is probably a much larger diurnal range in the Muhavura, Karasimbi area.

The changes in air temperature are not, however, constant and a great deal of difference can be found in sites only a short distance apart. Hedberg (1963) showed that at an altitude of 4,200 m. in the Teleki Valley (Mount Kenya), two stations 50 m. apart and only differing in altitude by about 5 m. showed a considerable difference in amplitude. The lower station being only half that of the upper. Although these figures were not recorded simultaneously or at a standard height above the ground they do show how important local variations in climate must be to the vegetation. The sudden change from one vegetation type to another in a short distance is in many cases probably entirely due to very local climatic conditions.

In March, 1966, the University College, Nairobi Zoology Department Expedition to the northern slopes of Mount Kenya carried out further measurements which although again not measured at standard height above the ground give a good indication of the climate in this quadrant of the mountain.

TABLE 1

TEMPERATURES MEASURED ON THE NORTHERN SLOPES OF MOUNT KENYA BETWEEN 18TH - 27TH MARCH, 1966

| | *Site A* | *Site B* | *Site C* |
|---|---|---|---|
| Mean Temperature | 6·8°C | 7·8°C | 4·8°C |
| Mean maximum | 14·4°C | 17·7°C | 9·8°C |
| Mean minimum | –0·6°C | –1·7°C | –1·2°C |
| Mean daily range | 15·5°C | 19·5°C | 11·7°C |
| Maximum daily range | 21·7°C | 25·0°C | 17·2°C |
| Minimum daily range | 3·9°C | 12·8°C | 7·8°C |
| Highest temperature recorded | 21·7°C | 23·3°C | 16·1°C |
| Lowest temperature recorded | –5·6°C | –4·4°C | –3·3°C |
| No. nights frost free | 5 | 1 | 1 |
| No. days observation | 11 | 11 | 8 |

Site A. Stream side 12,500 feet Kazita West Valley. Under *Euryops brownei* bush.

Site B. Ridge top 30 feet above stream course Kazita West Valley, 12,530 feet. Under ericaceous bushes.

Site C. Ridge overlooking Kazita West Valley, 14,000 feet. Shaded by *Senecio keniodendron*.

Data measured at two stations at 12,500 feet and one at 14,000 feet (3,811 m. and 4,268 m.) are shown in Table 1. It may be said of these figures that although the temperature range is close to that expected at this altitude, the number of frost free nights is higher than that experienced at these altitudes on other sectors of the mountain, indicating a climate that is milder by perhaps as much as 3°C. If the difference in amplitude recorded by Hedberg (1964) was a valley wall phenomenon it would appear in the new figures quoted above that the effect has here been reversed.

Platt (1966) has shown that at 4,750 m. on the Lewis glacier mean daily temperatures fluctuated over 13 days between 0·0°C and –1·9°C.

## Radiation

The major effect of increase in altitude is that the thinner atmosphere results in less heating of the air during the passage of solar radiation. Thus the isolation at ground level is far more intense, with a corresponding increase in outward long wave radiation. The most important element of this incoming radiation is the ultraviolet, the high intensity of which is probably reflected in the high percentage of leaves that are heavily pigmented, coriaceous, hairy or reduced in size.

Although during the day the outward radiation from the ground and vegetation is not very apparent, at night its effect is of great importance as an additional cooling agent at the surface (Geiger 1950). This phenomenon is one of the most important agents in determining the nature of night frosts and the accompanying microclimate at ground level, that will affect the lives of vertebrates and invertebrates that live within its influence.

Black bulb temperatures measured by the author at 3,811 m. (12,5C0 ft) registered between 70 and 77°C over 10 days.

Platt (1966) recently measured radiation on the Lewis glacier and has related total daily short wave radiation to the duration of daily sunshine. This varied from 300 Langleys with one hour of sunshine to 520 Langleys in 9 hours of sunshine. These figures are slightly higher than those recorded by Bergstrom on Ruwenzori which again underlines the effect of greater cloud cover on this western mountain.

## Wind

Unlike mountains at higher latitudes, high winds are uncommon in the alpine zone except under stormy conditions, which are generally uncommon. The only point at which they may be of some importance is in narrow gorges close to the peaks and at the foot of glaciers where cold night winds are an important factor in restricting the colonisation of newly exposed moraine deposits. The absence of strong winds greatly reduces the amount of wind blown organic debris carried to the peak regions and in turn restricts the arthropod fauna that would feed on this material. This is in strong contrast to the situation on the Himalayan range where Mani (1962) and Swan (1961) found that these materials were responsible for the existence of a rich invertebrate fauna close to the glaciers.

Wind measurements carried out by the East African Meteorological Department show that at 4,880 m. above Nairobi wind speed varies annually between 5·6 and 8·6 m./sec. Wind peaks occur in Oct.-Dec. and Feb.-Apr. with a calm period between April and September. The peaks roughly coincide with the lowland rainy periods. It has also been shown that there is a diurnal wind cycle in which night and early morning winds decrease almost to zero at about 14·00-16·00 hours (Platt 1966).

## Atmospheric Pressure

The fall in atmospheric pressure with altitude and the consequent depression in oxygen tension although probably having little effect on the vegetation must at least restrict or act as a stringent selection factor on the alpine fauna. The equatorial mountains do not rise to a height where vertebrate life is impossible, and areas over 14,000 feet on Mount Kenya have herds of resident zebra, just as the saddle of Kilimanjaro has a resident herd of eland, who spend much of the time at or above 15,000 feet. Mani (1962) has calculated the decrease in oxygen tension with altitude and shows that at 4,000 m. (13,120 ft) the percentage of oxygen tension that would be expected at sea level has fallen to 61·50% while at 5,000 m. (16,400 ft) it is 52·40%. Although arthropods are known to be able to live under conditions of very low atmospheric pressures and a high degree of hypoxia and anoxemia the effect on vertebrates must be important.

## MICROCLIMATE

When we speak of the afro-montane climate we always think in terms of the macroclimate, but as far as the plant and animal life is concerned it is the microclimate of individual niches and the general climate near the ground that is of the greatest importance. In a climate with large and regular diurnal temperature changes it is not so much the extremes, but rather the speed with which they fluctuate that is the main controlling factor on the fauna.

Geiger (1950) in considering the climate near the ground quotes the work of Maurer who found that the amount by which the ground temperature exceeds that of the air increases with altitude, a factor of obviously great significance to the microclimate in the equatorial mountains.

The effect of incoming radiation on the surface of the ground has been well illustrated by Scaetta (1934) who showed that at an altitude of 4,506 m. (14,780 ft) on Karasimbi, north of Lake Kivu, there was a striking difference between ground and air temperature. His figures are as follows:—

| | | |
|---|---|---|
| 12·00 hours | Free Air | 5·0°C |
| | Inside *Alchemilla* clump | 14·6°C |
| | Top layer of dry soil | 16·2°C |
| | Air-Ground difference | 11·2°C |
| 13·00 hours | Free Air | 3·5°C |
| | Clump of *Poa glacialis* | 17·4°C |
| | Dry lichens on lava plateau | 19·4°C |
| | Air-Ground difference | 15·9°C |

Klute (1920) carried out similar measurements at 4,150 m. on Kilimanjaro and recorded a difference of as much as 31·2°C between a bare rock surface and the air above. Kullenberg (1962) has shown that at an altitude of 4,200 m. on the Ruwenzori range a temperature difference of 10-12°C existed between the ground and the air 1·5 m. above. This difference was in spite of the fact that the measurements were made at midday in cloudy, rainy weather.

The speed with which the air and ground temperature change has been demonstrated by Coe (1967) working at 13,700 feet (4,176 m.) on the Mackinder Valley on Mount Kenya. In changeable weather the air temperature fluctuated from 48°C to freezing point in little more than 30 minutes. In the same manner, as the air temperature fell, so rapid reradiation from the ground led to rapid surface cooling. The greatest diurnal amplitude of ground temperature was recorded on 4th January, 1963, when it rose from −10·0°C at 02·00 hours to +14·0°C at 09·99 hours, a range of 24°C.

Mount Kenya, the Aberdares and Kilimanjaro are less susceptible than Ruwenzori to intense cloud cover during the day, but during wet periods the sun may be obscured by cloud or mist several times in a day. When this happens the air and ground temperatures are likely to fluctuate wildly, a factor of importance when considering the activity cycles of the alpine invertebrate fauna.

During the day the inward radiation tends to obscure the losses from outward radiation, but at night these rapid losses lead to accelerated cooling of the surface and in consequence this effect may be strongly felt by many of the micro niches occupied by animals. On clear unobscured nights, which are the rule rather than the exception on Mount Kenya this rapid cooling effect is to say the least dramatic. As intense as these effects may be, since the changes are only diurnal and not seasonal, the sudden lowering of temperature does not penetrate more than a few inches below the surface of the soil. In large part the protective insulating mechanisms that have been developed by the vegetation are fully utilised by the vertebrate and invertebrate faunas.

## VEGETATION

Since the alpine vegetation is so closely controlled by the climate, and the animal life of these regions is in turn dependent on the vegetation for cover, the main vegetation types will be briefly outlined. Although each mountain possesses its own endemic species, for the sake of simplicity species occurring on Mount Kenya will be enumerated.

### Moorland or Ericaceous Zone

The point at which any vegetation zone starts or ends depends on the mountain under consideration or even on what face the plants occur. For general purposes we may follow Fries (1948) and say that the lower limit of the moorland zone falls at 3,300 m. (10,829 ft) and may extend up to 3,500 m. (11,480 ft) or even higher depending on the prevalence of fire and the degree of shade afforded by valley walls.

The constitution of moorland plant associations varies with aspect but we may say that in general it is characterised by a fairly dense cover of *Erica arborea*, *Philippia keniensis*, *P. excelsa*, *Anthospermum usambarense*, *Adenocarpus mannii*, *Protea kilimandscharica*, and *Euryops brownei*. Between dense stands of these plants coarse tussocks of *Festuca* occur on sloping ground and valley bottoms. In the latter situation where the ground is very damp the main tussock is *Carex monostachya*.

### The Alpine Zone

This is a composite zone comprising the upper and lower alpine zones of Hedberg (1957) which extend from 3,500 m. (11,480 ft) to the edge of the Nival zone in the region of the peaks at 4,500 m. (14,760 ft).

The most noticeable element of the vegetation cover is the dense stands of tussock grasses, the main genera of which are *Festuca*, *Deschampsia* and *Pentaschistis*. The species occurring will depend on whether the ground is flat or sloping, wet or dry. Scattered over these grasslands are the giant lobelias and senecios so characteristic of the afro-alpine scene. On Mount Kenya the main species are the erect *Senecio keniodendron* and *Lobelia telekii* occurring on well drained ground and *Senecio brassica* and *Lobelia keniensis* in waterlogged areas. The latter regions are also covered with dense stands of *Carex monostachya* tussocks as in the moorland.

The most characteristic features of the Alpine zone are the erect grass tussocks, megaphytic senecios and lobelias. These are the conspicuous elements in the flora but by far the largest percentage of the alpine flora consists of low rosette plants that occur on open ground or patches of soil between the tussocks. The most noticeable of these being *Ranunculus*, *Swertia*, *Anagallis*, *Haplocarpha*, *Carduus* and *Haplosciadium*, all of which are characterised by their flat growth habit and stout short tap root. In large part this habit seems to be a response to alpine climatic conditions (Hedberg 1964, Coe 1967).

Ridge tops above 4,000 m. (13,220 ft) and old lake beds are virtually devoid of vegetation and are severely frost heaved by either needle ice or soil polygons. Valley walls show extensive signs of soil creep and solifluction. All these phenomena are a direct result of the marked diurnal temperature changes and the consequent rapid evaporation at ground level.

### Nival Zone

This zone occurs at the foot of the main peaks where signs of recent glacial activity can readily be distinguished (Troll 1958). Plant cover is sparse and the ground is covered by glacial moraines of graduated particle size.

## THE ALPINE FAUNA

Although a number of workers have collected animals in the alpine zone little attention has been paid to the importance of microclimate to animal life in these regions. Salt (1954) in his study of the Kibo saddle and Shira plateau of Kilimanjaro noted the predominant cryptozoic habit of arthropods and the important controlling influence of diurnal climate and radiation. Mani (1962) has studied the insects of Himalaya and has drawn attention to the similarities between arthropods on high mountains throughout the world. At the same time the problems faced by animals in these high latitudes are both seasonal and diurnal which produces an added complication in studying their ecology.

It is possible to consider the afro-alpine fauna in relation to the niches that are available to them for occupation in order that they may avoid the rigours of the equatorial montane climate.

### a. Dwellers in open ground

A number of creatures that live above the forest can survive diurnal temperature changes without the need for cover at night. Typical of this category are the larger mammals. The alpine duiker *Sylvicapra grimmia altivalis* occurs throughout the moorland and alpine zones and is found in dense vegetation where it is afforded some cover from predators and low night temperatures. One of its main adaptations to alpine life is that it appears to be largely diurnal in its habits. In these protected situations it is not only well hidden but is also less likely to suffer the low night temperature of valley bottoms. It is interesting to note that on the northern slopes of Mount Kenya this mammal is almost entirely replaced by the steenbok (*Raphicerus campestris*). The presence of this essentially lowland antelope may be attributed to the slightly milder climate of this side of the mountain and the gap in the forest that has allowed it access from the plains below (Coe and Foster, 1967).

One or more resident herds of zebra occur on the northern slopes of Mount Kenya and their droppings are found up to 4,300 m. The presence of these mammals may be explained in the same way as the steenbok.

Eland, buffalo and elephant have all been recorded as high as the main peaks of most of these mountains but except for the eland of Kilimanjaro they are not resident at high altitude and only enter the alpine zone when passing from one segment of the forest to another.

The number of warm blooded vertebrates that live in a situation where they are afforded little cover is very small indeed and in the majority of cases they occupy natural holes and shelters, however small.

b. Natural holes or shelters

The surfaces of all the East African mountains show signs of intense glacial erosion which in many cases can be traced as low as 9,500 ft (2,896 m.), and have not only been responsible for dissecting large valleys but have also laid down extensive moraines. Thus large boulder moraines, dissected and collapsed cliffs, eroded lavas and ashes have all provided shelter for a number of non-fossorial animals.

The most striking example of this type of niche is that of the Mount Kenya hyrax *Procavia johnstoni mackinderi* which occurs from 12,000 feet to the foot of the peaks in suitable rocky habitats. Its absence below this altitude can be attributed almost solely to the lack of suitable occupation sites through the less intense degree of glaciation at this level. These creatures are much larger than the lowland subspecies of *P. johnstoni* and have unusually long fur. They live in amongst the rocks and although in many cases they do not descend more than one metre below ground, this seems to be sufficient to protect them from low night temperatures.

Undoubtedly their social habit of "clumping" together in their quarters is an additional factor that enables them to survive so successfully at high altitude.

In the early morning these animals emerge soon after sunrise and bask lying on their sides. In this position they present a maximum surface of their bodies to the sun's rays and in addition by pressing their bodies to the rock can receive reradiated heat from below. It has recently been shown that the hyrax's body temperature may rise up to six degrees when basking. Just as in the lowland hyrax the alpine forms show a very distinct diurnal cycle of feeding and basking, which is in bright sunlight restricted to a few hours in the morning and the late afternoon (Sale 1965).

The Queen Elizabeth College Expedition to Mount Kenya (1965) measured temperatures inside hyrax burrows and found that the mean maximum over 4 days was 9°C and the mean minimum 0·6°C. At the same time the air temperature outside varied from a mean maximum of 9°C to a mean minimum of −4°C (Sale 1965, Coe 1967). Thus the temperature inside the burrow remained above freezing, albeit fractionally. This is a feature that is noted frequently, that although an animal may not be able to avoid cold it can select a niche that will only rarely descend to freezing point and under these circumstances it can survive.

It is interesting to note that on Ruwenzori the tree hyrax *Dendrohyrax arboreus ruwenzori* has left its arboreal habitat to live amongst the glacial debris of the alpine zone. This would not have been possible if a true rock hyrax *Procavia* or *Heterohyrax* had already occupied this niche. The presence of a rock hyrax on Mount Kenya and its absence on the nearby Aberdare range may partly be explained by the montane forest gap to the north of Mount Kenya through which it probably gained access to the alpine grasslands. This forest gap is absent on the Aberdares. In addition, however, the much less frequent occurrence of large moraine deposits on the much lower Aberdares would itself preclude successful colonisation by these animals (Coe 1962, 1967).

In spite of the basically diurnal habits of the Mount Kenya rock hyrax it is very active on bright moonlight nights, but this activity is probably related to sexual behaviour.

A number of predators also occupy natural shelters and being mammals and birds of reasonable size they are not so affected by diurnal temperature extremes. The leopard *Felis pardus* is the largest predator in the East African alpine grasslands and one or two pairs occur in most valleys. These animals are undoubtedly an important controlling factor on antelope and hyrax populations. Wild cat *Felis lybica* also occur on Mount Kenya and are particularly common on the northern slopes, where they live in holes under old eroded lava flows.

Small mammalian predators are uncommon on most of the mountains and records are very poor. Salt (1954) records the civet cat *Civettictis civetta* sub. sp. and the serval cat *Felis serval* from above 3,500 m. (11,500 ft) on Kilimanjaro. The Red River mongoose *Atilax palundinosus* was seen in the Gorges Valley on Mount Kenya at an altitude of 11,750 ft (3,582 m.) and a single specimen of the zorilla *Ictonyx striatus* was collected at 14,000 ft (4,268 m.) on the northern slopes of Mount Kenya in March, 1966. This was an unusually large specimen with very long fur that had been feeding on *Otomys* rats which it had scratched out of their shallow burrows (Coe 1967, Coe and Foster 1967).

A number of avian predators occupy cliff shelters where they can only receive minimal protection from night extremes. In the case of the Mackinders Owl *Bubo capensis*, since the bird is nocturnal it is probably not affected, though its young in the nest must need protection from at least one parent at night before they are fledged. Verreaux Eagle *Aquila verreaux* also occurs in the alpine zone where it feeds on hyrax and breeds in the Gorges Valley. Lammergeyer Eagle *Gypaetus barbatus* also feed on hyrax and have been seen in all valleys on Mount Kenya. As many as three birds have been seen in the air at one time in the Kazita West Valley (personal field observations). We know very little of the temperature conditions on cliff ledges but one suspects that the further the site is removed from the ground the milder the night temperature is likely to be.

c. Burrow dwellers

A number of creatures in afro-alpine regions are burrowers and in turn a number of other creatures take advantage of their fossorial activities as a means of obtaining a dwelling site. Burrows constructed by these creatures do not need to be very deep as the nightly frost does not penetrate very deep and a few inches is sufficient to avoid freezing (Coe 1967). Soil temperatures measured in the Mackinder Valley in January, 1963, showed that four inches below the surface the temperature did not vary more than +1 to +4°C, even when the air temperature fell as low as −10°C. The total daily range at this depth is not more than 3-4°C.

The commonest rodent in the moorland and alpine zones on Mount Kenya is the groove toothed rat *Otomys orestes*, other species or subspecies of which occur on the Aberdares, Kilimanjaro, Mt. Meru and Elgon. These mammals construct shallow burrows 5 cms. in diameter and which are seldom more than 30 cm. in total depth. In many situations they may burrow in the bases of ash deposits or in soft shallow soil. In dense *Festuca* tussocks and *Alchemilla* scrub their burrows do not penetrate the ground for more than a few cms. and run for the most part through the soft vegetation mat. Above 4,000 m. (13,120 ft) where the ground is often stony, except for the banks of streams and lakes where there is dense grass cover these rodents have left the ground to burrow into the leaf girdles of *Senecio keniodendron* (Coe 1967). In all these situations the night temperature does not fall below freezing although like the hyrax colonies, it may only remain fractionally above.

The other high altitude rodents of Mount Kenya are *Lophuromys aquilus* and *Dendromus insignis* which do not appear to burrow extensively themselves but rather occupy the old burrows of *Otomys* and other sheltered spots. The former species are of interest since they appear to be largely insectivorous.

A single genus of shrew that is endemic to Mount Kenya and the Aberdares is the mole shrew *Surdisorex polulus* which is a squat animal with a short snout and irridescent fur very like that of the European mole *Talpa europea*. Its fore limbs are equipped with long digging claws as are to a lesser extent the hind limbs with which they can excavate their burrows at the base of tussocks and in soft ground. Little is known of its habits but its burrows are shallow and descend just a few inches, to a point where the temperature will remain fairly constant and always above freezing point. Many of these mammals have been trapped at night which suggests that they are mainly nocturnal. It would be interesting to know if during their burrowing activities they feed on earthworms and beetle larva, particularly as these represent a source of food that is little exploited by other vertebrates.

At least three other species of shrew *Crocidura alex alpina*, *C. fumosa* and *C. turba zaodon* occur in the moorland and alpine zones but there is little information relating to their habits. Since however they are often trapped on *Otomys* runs it seems likely that they utilise other creatures' shelters.

It is interesting that such a comparatively large number of very small mammals should live at high altitude, for their very small bodies must make them very susceptible to the cold. If a shrew is caught in a live trap at night and left without bedding it can survive freezing temperatures for little more than an hour. Their great activity when they do emerge and the cryptozoic habit of arthropods must make food collecting comparatively easy, so that it may not be necessary for them to remain out of their shelters for very long. When the warm blooded creatures enter their sleeping quarters their own body heat must quickly raise the air surrounding them to an equable level, though when we remember that the soil in which they live seldom rises above 6°C their temperature regulation problems must be acute.

The only comparatively deep burrower on Mount Kenya is the giant mole rat *Tachyoryctes rex* whose burrows have been traced down to a depth of four feet. This species is replaced on Kilimanjaro and Mt. Meru by *T. daemon* but little is known of its habits. The presence of the Mount Kenya species is characterised by "mole hills" which are constructed in areas where suitable soil occurs. In places on the northern slopes a number of animals burrow in one spot until a mound up to 6 metres across is raised above the surroundings. These mounds can be spotted some distance away as their vegetation cover is an almost pure stand of *Alchemilla argyrophylla*, which gives them a grey-green appearance. These are the "earthworks" that some travellers have reported on Mount Kenya. Tunnels have been traced for up to 50 metres from these mounds. When excavating the main mound it has been found that these mammals utilise one or more chambers within the burrow system as a latrine where they defeacate, urinate and store waste vegetable material. The heat from these mounds is considerable and the rats build grass nests alongside in which it is presumed that they sleep. It is not known if this is a general habit in the genus, but it must be an important way of avoiding the low temperatures of the alpine soils. One of these dung piles measured 12°C and was full of dipterous larvae, the adult of which has not yet been identified (Coe and Foster 1967).

### d. Rocky ground

Much of the alpine zone is covered with glacial and scree debris, particularly at altitudes over 4,000 m. (13,120 ft) where heavy frost heaving prevents or restricts plant colonisation. Salt (1954) has pointed out that in the alpine desert of Kilimanjaro these stony habitats are important regions for occupation by invertebrates. This is also true of Mount Kenya but the less porous nature of this mountains surface makes vegetation niches of equal importance. The only animal of any size that lives in this habitat on Mount Kenya is the alpine meadow lizard *Algyroides alleni*, which is, on the northern slopes joined by the small lizard *Mabuya irregularis*. In this type of situation although animals gain heat rapidly during the day, they will also lose it rapidly at night. In selecting a rocky habitat the size and shape of the rock is also important for large rocky masses will hold their heat longer but take longer to heat up, while small rocks and flakes will heat up very rapidly so that the air below them may have reached 35-40°C by 10·00 hours.

The short period available for feeding in these bare habitats has been noted by Swan (1952) working at 4,120 m. on Mt. Orizaba in Mexico. He found that the lizard *Sceloporus microlepidotus*, which ranges from low elevations to 4,500 m. is forced to confine its activities to about four hours each day. This appears to be quite sufficient for feeding since he found that lizards dissected after two hours' activity had already filled their stomachs. As with the lizards of Mount Kenya *Sceloporus* always selected rocks over 8 inches thick for occupation. The shade temperature in this situation was fairly constant at about 5°C, while for short periods they would be active in temperatures that ranged from 27-40·6°C. Along the shores of tarns on Mount Kenya a green coloured form of *A. alleni* is sometimes active in the hottest part of the day but this activity consists mainly of a quick dash from shelter in the open after which it will quickly return to cover.

The author measured temperatures below and on the surface of a flat tilted rock (126 cm. x 90 cm.) at 12,500 ft on the northern slopes of Mount Kenya. The rock was situated on damp, slightly sloping ground which was frost heaved and covered with gravel. The surrounding vegetation was *Festuca pilgeri* tussocks and scattered clumps of *Helichrysum declinatum.* A number of fertile alpine meadow lizard eggs had been laid below this rock which was 23 cms. thick at the centre. Evidence of regular occupation by lizards was provided by large quantities of insect remains below the rock. At 15·00 hours in 50% cloud cover the air temperature was 10·2°C, the surface of the rock 31·4°C and the air below varied from 12·4-15·8°C. Shaded humidity of the rock surfaces was 32% while that recorded within the rock shelter was 75%. At night when the air temperature fell to −2°C the temperature of this shelter did not fall below 0°C. In the early morning before the sun had warmed the ground lizards could be collected from their shallow hiding places in a completely torpid state.

In this type of habitat where at sunset there is a rapid change of temperature it seems possible that an important advantage of such a niche is the water that is made available from condensation when the temperature falls so rapidly.

The period during which insects can be active in such areas must be very small, for at night the intense cold renders them incapable of movement while during the day except for a short period after sunrise and just before sunset the ground temperature is far too hot and the humidity too low. Undoubtedly it is these two factors more than any other that account for the high percentage of arthropods exhibiting a sedentary and cryptozoic habit. As Salt (1954) has pointed out after his visits to Mount Kenya and Kilimanjaro, in spite of the large number of insect species that can be found under stones, in soil or amongst vegetation, very few are ever seen walking about, while less still are actually seen on the wing. On Mount Kenya the only insects regularly seen flying are chironomids over *Lobelia keniensis* rosettes and the lycaenid butterfly *Harpendireus aequatorialis* over *Alchemilla.*

Considering the short period of activity for insects each day it is remarkable that Augur Buzzard pellets from Mount Kenya analysed by Dr. J. B. Foster contained carabid beetle elytra in almost every sample examined, yet during a two week stay in the area from which the pellets were collected the author only saw two specimens walking in the open. Either this confirms the high degree of acuity of this bird's vision or suggests that its main period of activity coincides with that of the carabids.

In spite of the many apparent disadvantages of this habitat there is no doubt that it forms one of the most important niches in the alpine zone if one includes invertebrates living under plant cushions as well as rocks. Salt (1954) noted that while half of his invertebrate collections on the Shira plateau came from a rocky habitat almost the whole collection from the Kibo saddle were derived from rocks or plant cushions associated with them. This does not mean to say that this is the most important habitat, for where more favourable and humid situations exist in grass tussocks, *Lobelia* and *Senecio* plants, these are fully utilised. Above 4,300 m. (14,104 ft) where exposure greatly restricts vegetable growth rocky sites are the only situations available for occupation, so that at extreme altitude these niches must be considered an important element in the microclimatic picture.

Working on Mount Kenya with the author in March, 1966, Harmsen and Jabbal recorded the following insects as important constituents of the rock fauna. *Amphitmetus sulcipennis* (*Curculionidae*), *Carbomorphus catenatus* ssp *bastinelleri* (*Carabidae*), and several species of *Harpalinae* and *Staphylinidae* all of which showed a cryptozoic habit and restricted activity cycles. The tenebrionid beetle *Phrynocolus arturium* was collected from open soil and among rocks and small patches of vegetation. These creatures showed activity including mating at 12°C and their larvae were collected in the same situations (Harmsen and Jabbal 1967).

e. Plant shelters

Except at extreme altitude the most important sites open for occupation by invertebrates is the vegetation. It has been shown that most of the alpine plants have succeeded in overcoming the diurnal temperature extremes by means of special insulating mechanisms (Hedberg 1964, Coe 1967), and it is these situations that form the most important invertebrate alpine shelters.

It has already been pointed out that by far the commonest growth form in the alpine zone is the rosette habit, which in itself provides limited protection below its leaves. The most highly utilised sites however are the large grass tussocks, and the giant lobelias and senecios.

(i) *Grass tussocks*

An individual tussock of *Festuca* consists of three zones, the outer dry and usually spreading leaves, an inner or medium area of compacted damp grass stems, and a lower basal disc which is very wet and from which the new shoots and roots arise. Temperatures measured by Hedberg (1964) in a *F. pilgeri* tussock in the early morning showed that when the temperature amongst the outer leaves was −5°C that of the lower compacted area was still +2·5°C and the upper rhizosphere of the root system +3·0°C.

In March, 1966, the author carried out further measurements in a tussock with a "Light" electrical thermometer. The results are shown in Figure 1. It will be noted that the outer leaf area fluctuates violently while the leaf bases do so moderately. The basal disc remains virtually constant with a range of little more than 2·1°C as against the outer leaf range of 13·3°C. Over the period that these records were made the air temperature did not fall below freezing.

Any creature that occupies these tussocks has in 1-1·5m. a gradation of temperature that it can utilise for its main activities. A large number of beetles live in this situation and appear to feed within them and seldom move outside. Harmsen and Jabbal (1967) recovered the adults and larvae of *Parasystates elongatus* (*Curculionidae*) from amongst the damp leaf bases where the temperature remains constant. They also recovered the adults of *Senecobius basirufus* (*Curculionidae*), *Amphitmetus sulcipennis* (*Curculionidae*), and *Carabomorphus catenatus ssp jabbalae* (*Carabidae*). Since the two subspecies of the latter species have been

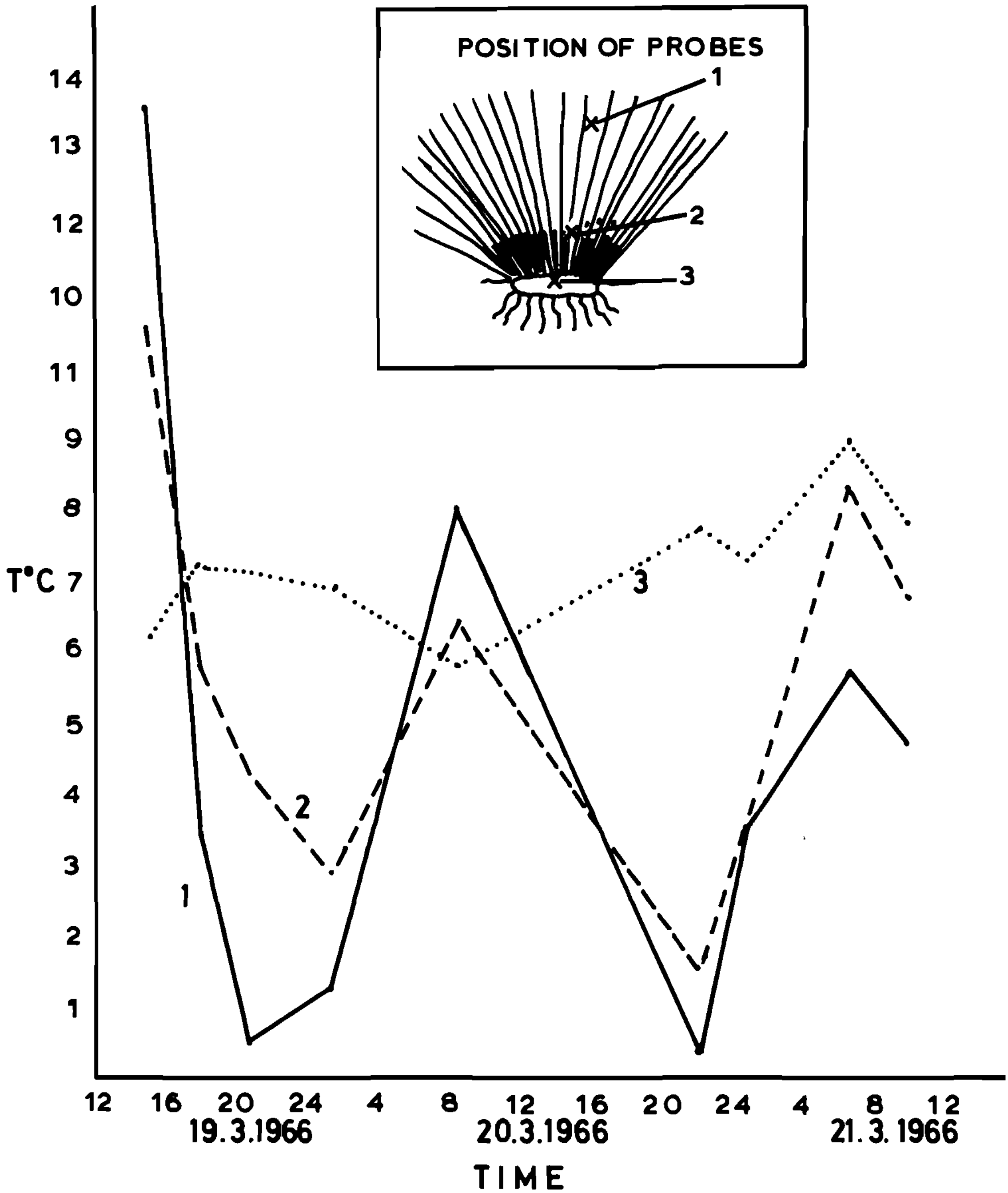


FIGURE 1
Temperature variations within a tussock of *Festuca pilgeri*.

recorded from the alpine zone of Mount Kenya it would be of interest to show that *bastinelleri* occupies a rocky habitat while *jabbalae* lives exclusively in vegetable shelters.

One of the most interesting observations recorded by Harmsen and Jabbal (1967) is their discovery that the larvae of *Gorgopis* sp and *Metarctia* sp. (Lepidoptera) construct silken tubes which run between the grass stems from the basal to the outer leaves. Small spines on the sides of the pupae allow them to migrate up and down these tubes as the air temperature changes. Thus in the morning and late afternoon they are found between the outer leaves while during the hotter parts of the day and at night they move to the more constant temperature of the leaf bases. These moths, several of which are as yet undescribed showed great nocturnal flight activity at 12,500 feet. On nights when the temperature did not fall below +1 °C these insects flew in large numbers and aggregated around pressure lamps, while if the temperature descended only one degree below freezing no moths were seen on the wing.

A number of species of Diptera also show interesting diurnal movements within the grass tussocks. At sunset large numbers of flies can be seen sitting on the ends of the tussock leaves, and if the temperature does not fall below freezing they will remain in this situation until sunrise the next morning. If the temperature falls to below freezing they are too cold to actively seek shelter, so release their grip on the grass stem and fall down into the interstices of the tussock. They will remain here until the next day when they can be seen slowly climbing the grass stems to reach the tip, after a short period of basking they fly off. This is particularly common along stream sides, and the flies mainly fly a short distance and settle on streamside vegetation.

These grass tussocks are also important as a nesting site for the Hill Chat *Pinarochroa sordida earnesti* and rarely for the Scarlet Tufted Malachite Sunbird *Nectarinia j. johnstoni.* The Hill Chat constructs a domed nest of woven grass with a lateral opening. The nest is lined with feathers and the downy pappus of giant senecio seeds. Temperatures in a nest situated at 12,500 feet on Mount Kenya were studied in March, 1966, by the author. These measurements are shown graphically in Figure 2. It will be noted that although the air temperature fell to −1·8°C the eggs did not register any lower than +9·9°C with a range over 3 days of about 8·7°C. The range between the outer leaves of the same tussock was 22·2°C over the same period. Thus although the female cannot maintain her eggs at the daytime level of 15-19°C she can prevent them falling below about 9°C at night. Since this bird ranges between 7,000 feet and 15,000 feet on the northern slope of Mount Kenya we hope shortly to investigate the possibility of incubation time being increased with altitude.

On the Aberdares the only endemic alpine snake in East Africa is *Vipera hindei* which also lives inside grass tussocks and is commonly seen basking between the upper leaves during the early morning.

### ii. *The Giant Lobelias*

Unlike their erect forest counterparts the alpine *Lobelia spp.* occur as sessile rosettes that may be solitary or connected together by underground rhizomes. All species so far investigated show nocturnal sleep movements of the rosettes closing into "night buds", which

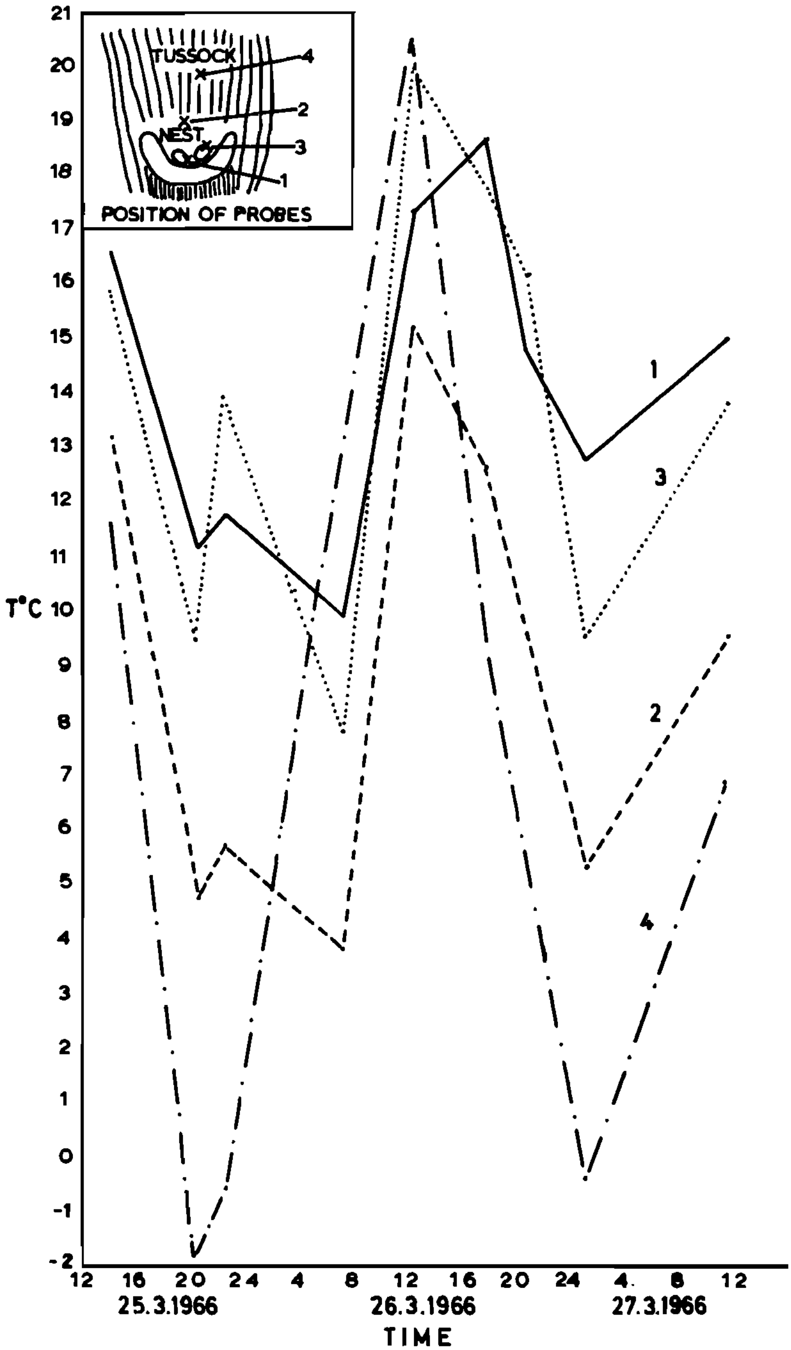


FIGURE 2
Diurnal temperature changes in the nest of an incubating Hill Chat (*Pinarochroa sordida*).

not only afford protection to their growing points but also to their invertebrate inhabitants. Hedberg (1964) recorded a temperature of $-3 \cdot 5$°C on the surface of an *L. teleki* rosette in the early morning while that recorded inside the folded leaves of the centre was $+1 \cdot 0$°C. The dead leaves at the bases of these rosettes are persistent and provide an insulating frill which protects the portion of the stem projecting above the ground.

TABLE 2

*Lobelia telekii* ROSETTE, KAZITA WEST VALLEY, 12,500 FT.

Probe 1. Growing point at centre of rosette.
2. Side of compacted centre of rosette.
3. Between leaf bases of rosette.
4. Centre of rhizome just below rosette.

| *Date* | *Time* | *Probe* 1 | *Probe* 2 | *Probe* 3 | *Probe* 4 |
|---|---|---|---|---|---|
| 27.3.66 | 17·00 | 6·2 | 7·6 | 6·1 | 7·9 |
| | 17·50 | 6·2 | 7·6 | 6·4 | 8·5 |
| | 20·00 | 6·5 | 5·8 | 6·2 | 6·2 |
| | 07·45 | 5·2 | 7·6 | 7·4 | 7·6 |
| | 09·40 | 5·3 | 4·4 | 4·4 | 6·2 |
| | 13·20 | 6·7 | 9·4 | 9·4 | 14·4 |
| | 14·25 | 7·6 | 10·8 | 10·4 | 15·2 |

(Temperature °C)

Temperatures measured by the author at 12,500 ft. on Mount Kenya for *L. telekii* are shown in Table 2. It will be noted that throughout the period of observation temperatures in different parts of the rosette did not fall below freezing although the air fell to below freezing on the night of 27.3.1966. Similar data recorded for *L. keniensis* is shown graphically in Figure 3. Temperatures within the rosette did fall to freezing point but did not go below, a critical factor when considering occupation by invertebrates.

The leaves of the *L. keniensis* rosette are broader than that of *L. telekii* and in overlapping they form a collecting area for water. These pools of water are rather viscous and since they do not seem to change their level even in periods without rain, much of the fluid is probably secreted by the leaf bases of the rosette. Certainly when a rosette is dissected the leaf bases are coated with a large blob of transparent mucus. These small pools are occupied by large numbers of chironomid larvae (*Diptera: Nematocera*) which in the imaginal stage hover as small clouds over the rosettes. The Scarlet Tufted Malachite Sunbird feeds extensively on these flies. It has been suggested by previous authors that the presence of this mucus may lower the freezing point of the water and in this way protect the plant from ice damage (Hedberg 1963, 1964; Coe 1967). At night when extensive ice forms around the *Lobelia* rosettes the "pools" freeze with only a thin layer of ice on top and against the outer leaves. Temperatures measured at 10.15 p.m. by the author when the air temperature was $-1 \cdot 3$°C gave readings

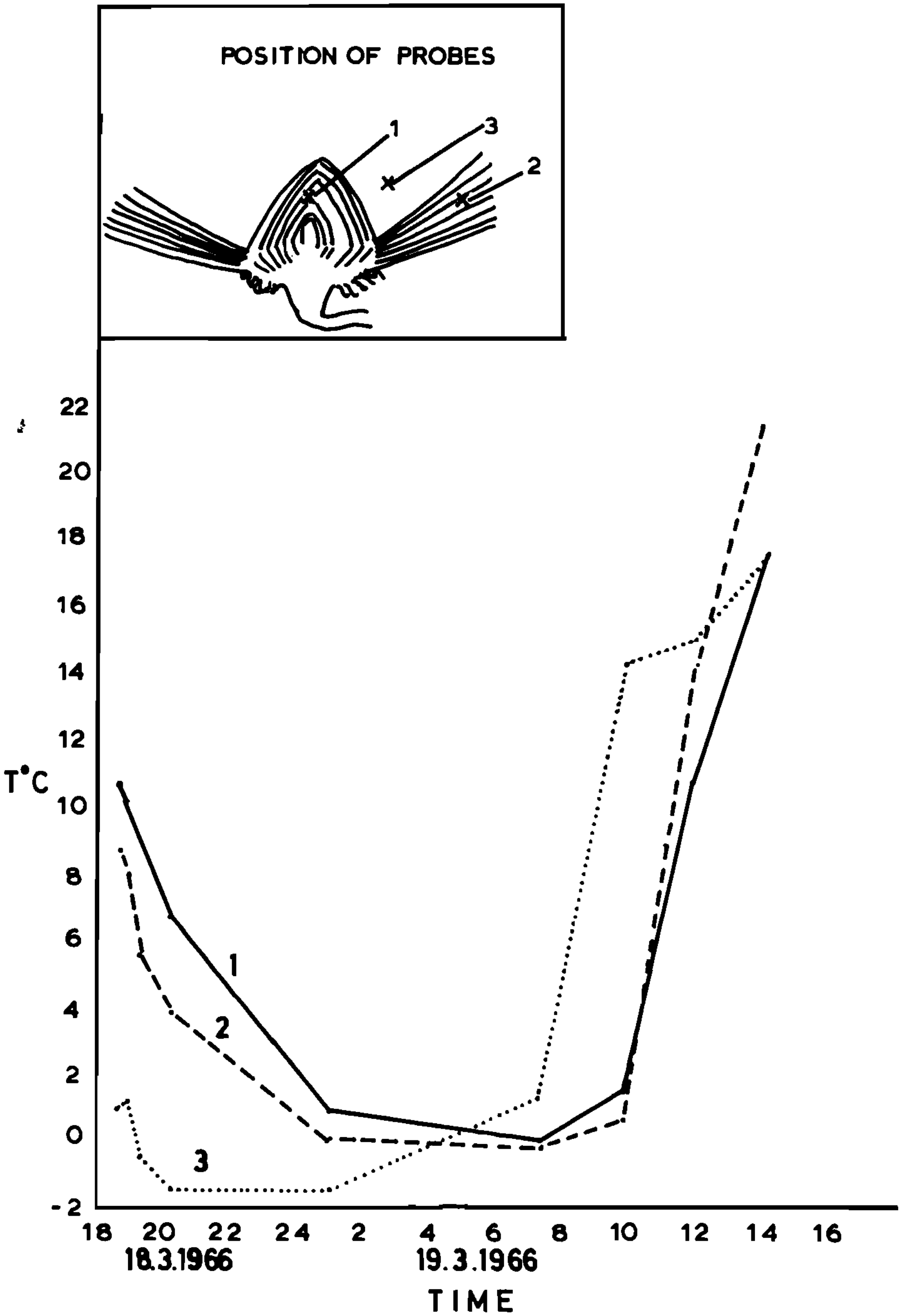


FIGURE 3
Diurnal temperature changes in a rosette of *Lobelia keniensis*.

FIGURE 4
Rosette of *Lobelia keniensis*. Note the pool of water between the leaves and a single specimen of *Gorgopis* sp.

of $-0 \cdot 8$°C close to the surface of the water and $+5 \cdot 3$°C amongst the leaf bases at the bottom of the "pool". In spite of the sub zero temperature at the surface no ice had been formed (Figure 4).

Harmsen and Jabbal (1967) have recorded the presence of adults, larvae, and pupae of *Cossonus frigidus* (*Curculionidae*) between the leaf bases of *L. keniensis* where the temperature never falls below $0 \cdot 0$°C.

When these rosettes flower the centres elongate to produce a long narrow inflorescence up to $1 \cdot 5$ metres long. The flowers are protected by bracts which are probably sufficient protection to prevent the ovaries embedded in the bract bases from freezing. The bracts of *L. keniensis* are short and broad and their bases enclose the ovary, while the bracts of *L. telekii* are long and narrow and fringed with hairs. The latter do not enclose the ovary in the same way as that of *keniensis* but their greater length probably provides sufficient insulation. Temperatures fell to $-2 \cdot 4$°C, the base of the corolla was still $3 \cdot 3$°C while the centre of the hollow

FIGURE 5
A stand of *Senecio keniodendron* at 13,000 ft in the Kazita Valley, Mount Kenya. Note the thick insulating layer of persistent leaves below the rosette. A single *Lobelia telekii* inflorescence can be seen to the left and *Festuca* tussocks in the background.

stem was +4·0°C. This situation is exploited by a bibionid fly (*Phoria* sp.?) which lives within the corolla of a *Lobelia* flower where it both feeds and reproduces, both adults, eggs, larvae and pupae being found in one flower. These insects though fully winged seldom fly and are utilised by the Scarlet Tufted Malachite Sunbird which runs up the *Lobelia* inflorescences like a Tree Creeper to feed on them. The lower bracts of the mature flowers are torn into narrow ribbons by the claws of these sunbirds.

iii. *The Giant Groundsels*

The other large group of plants so characteristic of afro-alpine regions and used extensively by animals for shelter are the megaphytic *Senecio sp.* On Mount Kenya three megaphytic species occur. The first two are erect forms up to 5 metres which branch sparsely and bear their rosettes at the end of long branches. *Senecio battescombei* occurs up to 11,500 feet (3,506 m.) at which altitude it is replaced by the truly alpine species *S. keniodendron*. The high percentage endemism in this genus provides a large percentage of the mountains with their own distinctive species but their growth forms are very similar. The other species on Mount Kenya is *S. brassica* whose habit is reminiscent of a *Lobelia* since the plant occurs as a sessile rosette from an underground or detritus covered stem.

As we have seen with the *Lobelia sp.* the giant senecio rosettes also close at night as "night" buds. The degree of closure depends on the degree to which the temperature falls (Coe 1967).

In *S. keniodendron*, the stem is covered by a thick corky bark while the dead rosette leaves are persistent and form a long "leaf girdle" over the stem and bark. The average diameter of the stem is 15 cm., the cork layer is up to 25 cm. and the leaf girdle up to 55 cm. in diameter. Thus along any one radius the stem is protected by 4·5 cm. of cork and an additional 15 cm. of leaf girdle. This effective insulating layer is utilised extensively by invertebrates and vertebrates. Birds use them frequently as roosting and nesting sites. It has already been pointed out that at high altitude where the percentage vegetation cover falls the groove toothed rat (*Otomys orestes*) makes its burrows in the leaf girdle (Figure 5).

Temperatures measured on a specimen of *S. keniodendron* at 12,500 feet on Mount Kenya are given in Table 3. The air temperature fell to $-0\cdot7$°C while the temperature within the leaf girdle was $+5\cdot3$°C and that of the rosette growing point $+8\cdot2$°C. Hedberg (1964) found in the early morning that with an air temperature of $-4\cdot0$°C that of the central leaf core was $+1\cdot8$°C, the temperature of the surface of the leaf girdle $-5\cdot0$°C, and the inside $+3\cdot0$°C. Thus birds, mammals and insects that penetrate between the leaves of the rosette or the leaf girdle are in little danger of the temperature falling lower than $+2\cdot0$°C.

TABLE 3

*Senecio keniodendron* (8 FEET HIGH), KAZITA WEST VALLEY, 12,500 FEET (28TH - 29TH MARCH, 1966)

| | 19·00 | 22·00 | 08·20 |
|---|---|---|---|
| Air temperature | 2·1 | −0·7 | 1·0 |
| Ground temperature | 3·2 | −0·1 | 0·8 |
| Leaf surface | 1·1 | −0·8 | 3·4 |
| Inside of leaf rib | 1·7 | −1·1 | 3·8 |
| Growing point | 8·2 | 4·2 | 0·0 |
| Inside leaf girdle | 6·3 | 5·3 | 4·4 |
| Leaf bases | 6·4 | 4·3 | 2·2 |
| Base of stem | 4·2 | 5·3 | — |

(Temperature °C)

The cabbage groundsel (*S. brassica*) grows on Mount Kenya in association with *Lobelia keniensis* on waterlogged ground. It also closes its leaves at night and the undersides of the leaves are covered with a dense tomentum which must also act as an additional insulating agent. Their procumbent rhizome-like stems that run below or actually on the surface of the soil are covered with a dense frill of dead leaves, and a number of invertebrates and rodents use this situation as a shelter. Temperatures recorded by the author at 12,500 ft are given in Table 4 and again clearly demonstrate the insulation afforded to the growing point by the leaves, and to the stem by the persistent leaf girdle. When the temperature at night fell to −1·4°C that of the leaf girdle remained at +5·4°C, the stem at +7·2°C and the growing point at +8·4°C. Just as the leaf frills of *S. keniodendron* were used by birds and mammals, Coe and Foster (1967) recorded the first afro-alpine record of a dormouse *Graphiurus* (*Claviglis*) *murinus* living in the bases of these plants in March, 1966.

TABLE 4

*Senecio brassica* ROSETTE, KAZITA WEST VALLEY, 12,500 FT.
(28TH - 29TH MARCH, 1966)

| | 18·50 | 20·00 | 07·50 | *Range* |
|---|---|---|---|---|
| Air temperature .. .. .. | 1·9 | −1·4 | 1·1 | 3·3 |
| Ground temperature .. .. | 5·2 | −0·2 | −0·2 | 5·4 |
| Between rosette leaves .. .. | 1·4 | −1·2 | −1·4 | 2·8 |
| Leaf bases .. .. .. | 9·2 | 5·8 | 1·3 | 7·9 |
| Inside leaf rib .. .. .. | 3·3 | −1·5 | 2·4 | 4·7 |
| In tumentum .. .. .. | 6·8 | −0·8 | −1·2 | 8·0 |
| Upper leaf surface .. .. | 10·8 | 1·2 | −1·2 | 12·0 |
| Within leaf girdle .. .. | 8·4 | 5·4 | 1·1 | 7·3 |
| Within stem .. .. .. | 8·4 | 7·2 | 3·0 | 5·4 |
| Within growing point .. .. | 12·2 | 8·4 | 11·9 | 3·8 |

(Temperature °C)

Since these plants occur on damp boggy ground the mammals only seem to visit the area for purposes of feeding but it does seem possible that creatures such as the dormouse that construct their dwellings above ground may be more or less permanent residents. The high density of mammals in these areas is illustrated by the author catching 22 mammals on one night in 22 bucket traps (Coe and Foster 1967).

iv. *Other vegetation niches*

Much of the alpine zone is occupied by dense stands of *Alchemilla* which provide a source of food for a number of mammals and cover many invertebrates. The larvae of the lycaenid butterfly *Harpendireus aequatorialis* feed exclusively on these plants, and, being one of the few insects whose adults fly readily during the day, many Scarlet Tufted Malachite Sunbirds gather to feed on them. Harmsen and Jabbal (1967) collected a number of specimens of *Afrotroglorrhynchus nivalis ?* (Curculionidae) from stands of *Alchemilla johnstonii.*

Many other plants have developed features that must be of great importance in protecting them from excessive radiation. Perhaps the most obvious examples are the brilliant white capitulae of many *Helichrysum* sp. that occur in afro-alpine regions. There seems little doubt that these flowers must reflect a large amount of the incoming radiation. At night these flowers also close into night buds when the reproductive parts must be protected from frost. During the day or in bright sunlight, when the air temperature was 13·9°C the centre of a *Helichrysum declinatum* flower at 12,500 feet was 26·4°C, while the surface of the flowers measured 19·1°C. At night the inside of the bud registered +1·5°C while the air temperature was −1·4°C. A number of small insects live inside these flowers or at least utilise them for night shelter.

f. AQUATIC HABITATS

The temperature regime of the afro-alpine aquatic habitats is far more stable than terrestrial habitats. There are, however, a number of interesting instances of the effect of diurnal changes.

Almost all the streams on Mount Kenya are permanent water courses flowing over rocky bottoms with frequent small rapids. These waters contain a large number of aquatic insects the commonest of which are the larvae and pupae of *Simulium dentulosum form macabae*. These insects occur in very large numbers in all streams, particularly in fast shallow water. In spite of the large number of immature stages, however, we have never succeeded in catching more than three adults and they have never been seen on the wing in the alpine zone. At the head of the Teleki Valley two streams flow 5 metres apart until their confluence at about 4,200 m. One stream arises from the Tyndall glacier and the other from the Lewis glacier. When visited by the author in January, 1958, it was noted that the Tyndall stream had dense vegetation along its banks and contained abundant *Simulium* larvae while the Lewis stream had little vegetation along its banks and appeared to contain no *Simulium* at all. At midday the temperature of both streams was about the same, 4·6°C. It was not until the area was visited in the early morning that it was noted that the surface of the Lewis stream freezes while that of the Tyndall a few metres away remains free of ice. The explanation of this phenomenon was found by following the streams to their sources. The Tyndall stream flows underground almost from the foot of the glacier while that from the Lewis flows for most of its course over a solid rocky bottom. Thus at night the Lewis stream is rapidly cooled as it flows over rock that is rapidly losing heat to the atmosphere, but the Tyndall stream flowing underground remains above freezing since the nightly frost does not penetrate more than a few inches, even at this altitude. Just as in other microclimates at high altitude, being fractionally above freezing makes all the difference whether or not animal life can survive.

Very few amphibians have been recorded from the true alpine zone of the equatorial mountains. No amphibians had been collected at high altitude on Mount Kenya until the author collected a large number of specimens of *Rana wittei* from the Kazita valley at 12,500 feet. Their presence is another good indication that the climate is milder on this sector of the mountain. These amphibians lived in water that showed a range over seven days from 3-13°C. They lived both in the water, under banks, and amongst vegetation along the banks. Their tadpoles (5 cm.) were recovered from deep pools. The adults were heard calling during the late afternoon and on several nights when the air temperature was below freezing.

The alpine zone of Mount Kenya is well known for its large number of lakes and tarns. Most of these are situated above 4,000 m. (13,120 ft) where the effects of glacial erosion have been most intense. Their waters seldom rise above +6°C, particularly in the larger lakes where there seems to be little circulation. The only major feature of reaction to diurnal temperature change is the vertical migration of the large copepod *Maraenobiotus* noted in the Hall tarns. These tarns are very clear and when surveying their boundaries from a rubber dinghy it was noted that while in the early morning no copepods could be seen, by 11·00 hours the surface of the water became quite red as large numbers of copepods rose slowly to the surface film. In the afternoon the copepods began to sink back to the bottom of the tarn. This activity must either be related to the heating of the surface film (which could not be detected) or to the fact that the bright red fat globules in these animals may be able to absorb radiation by lying close to the surface.

## ADAPTIVE TRENDS IN THE AFRO-ALPINE FAUNA

We have seen that the major limiting factor on the alpine fauna is the intense radiation, low night temperatures, high day temperatures at ground level, and the rapidity with which the temperature and humidity change from one extreme to another.

There is good reason to suppose that many morphological features of the vegetation are important in protecting it from intense radiation, and although there is little evidence one suspects the same to be true of the invertebrate fauna. Salt (1954) has cited the highly reflective surfaces of many beetles on Kilimanjaro as protection against radiation and this is also true of the carabids and curculionids of Mount Kenya. All the weevils of Mount Kenya *Parasystates*, *Cossonus*, *Seneciobius*, *Amphitmetus*, and *Afrotroglorrhynchus* possess inflated elytra whose enclosed air must have an important insulating function.

The predominantly dark colours of many alpine insects could also be important in heat absorption. In the early morning before the sun's heat is too intense it would be an advantage to be able to absorb heat quickly in order that the animal could complete its main period of activity before the ground becomes too hot. The dark colour of the lizards could operate in the same way. Certainly the lowland *Agama* lizards possess a dark colouration in the early morning, until their bodies have warmed up when they assume their brighter behavioural patterns.

The mammals of the alpine zone are on average larger than their lowland counterparts (*Procavia*, *Otomys* and *Tachyoryctes*) and without exception their fur is longer and denser. In addition their activity cycles are adapted to the diurnal climate even though their temperature control problems are not so acute. Analysis of Augur Buzzard and Mackinders Owl pellets (Coe and Foster 1967) show that *Otomys* forms a large part of their diet. Since the former is diurnal and the latter nocturnal this indicates that this rodent must be almost equally active day and night. Trapping figures though indicate that on nights of severe frost far less small mammals are active.

The disadvantages of the alpine climate are offset by the availability of food at a constant though low level throughout the year. Breeding can similarly take place throughout the year though *Procavia* does seem to have a breeding season (Coe 1962).

As we have already seen, although temperature changes are severe, since the effect is diurnal and therefore short term, severe freezing at the surface of the ground does not penetrate more than a few inches into the soil or the vegetation and in this way it is possible for vertebrates and invertebrates to avoid daily or nightly extremes by utilising comparatively shallow shelters. Once within these niches the majority of invertebrates have adopted a cryptozoic habit which keeps them within or close to the comparatively constant microclimate of their shelters.

It is well known that the insect fauna of high mountains throughout the world show a high proportion of brachypterous and micropterous forms.

Mani (1962) has pointed out that on NW Himalaya 50% of the insect species occurring above the timber line are brachypterous or apterous, while this figure rises to 60% above 4,000 m., and even those that do possess wings seldom use them. Salt (1954) has made a similar observation in relation to the alpine insect fauna of Kilimanjaro where he found that of 14 species of pterygote insects collected in the alpine desert 12 were flightless in one or both sexes. Similar observations have been made on the insects of Ruwenzori (Edwards 1939) and general high mountain Carabidae (Darlington 1943) which also show reduction in average size with altitude in contradistinction to the mammals. The function of this flightless tendency is still unclear though the frequency with which the female is brachypterous and the male winged may suggest that the evolution of isolated montane species has been accelerated by the retention of this tendency in the females while the males remaining winged assures that gene flow will be maintained within the isolated population.

In avoiding climatic extremes it is clear that some vertebrates and almost all invertebrates must either leave their sheltered niche or possess very definite activity patterns that are closely related to the climates changeability. This is certainly true of the Carabidae, Chironomidae, Tipulidae, and Lepidoptera of Mount Kenya which all show early morning and to a lesser extent late afternoon activity. This fact that is accentuated by the fact that the Scarlet Tufted Malachite Sunbird will feed on the wing in the early morning and late afternoon but in between resorts to catching its food in amongst the leaves of the giant lobelias and senecios. Mani (1962) clearly demonstrated that most insects showed activity cycles that were restricted to the early morning or late afternoon or both.

The alpine fauna by means of cryptozoic habits, aptery in insects, and restricted activity cycles in both vertebrates and invertebrates have succeeded in effectively colonising and at the same time avoiding the drastic climate of these regions.

## SUMMARY

1. The equatorial high mountains are characterised by a diurnal temperature regime of high day temperatures and low night temperatures.
2. Rainfall at high altitude roughly follows the lowland pattern of a long and short period. Rain is in general more evenly distributed throughout the year.
3. The variation of rainfall with aspect coincides with the depth and distribution of vegetation belts.
4. Large variations in humidity are recorded at ground level.
5. The temperature regime at high altitude is described and it is shown that considerable local variation occurs. Radiation data recorded on the Lewis glacier is also presented.

6. The most important feature of the microclimate is the great difference between air and ground temperature during the day, and the speed with which these temperatures change.
7. The main plant constituents of the Ericaceous and Alpine zones are briefly described.
8. Hyrax burrows maintain a minimum temperature of $+0{\cdot}6$°C while the air outside was $-4{\cdot}0$°C.
9. In spite of sub-zero air temperatures the soil at a depth of 6″ shows a very small range which never descends to freezing. This fact is employed by *Otomys* and *Tachyoryctes* which burrow in alpine soils.
10. Open rocky ground forms a very important niche for arthropods and some vertebrates at high altitude. Temperatures of these habitats are enumerated.
11. Most arthropods at high altitude adopt a cryptozoic habit and restrict their activity to a few hours after sunrise and before sunset.
12. Grass tussocks, giant *Senecio* and *Lobelia* plants form important occupation sites for vertebrates and invertebrates. The insulating properties of the alpine vegetation is fully exploited by the fauna.
13. Temperatures measured inside these plants demonstrate their effective insulation mechanisms.
14. Low night temperatures of Hill Chat eggs are described.
15. A number of aquatic animals are shown to be sensitive to diurnal temperature changes.
16. Adaptive trends in the alpine fauna are briefly discussed.

## ACKNOWLEDGMENTS

Much of the work described in this paper was carried out in conjunction with my colleagues in the Department of Zoology, University College, Nairobi. For both assistance in the field and discussions I am particularly grateful to Dr. J. B. Sale, Dr. R. Harmsen, Dr. J. B. Foster, Dr. A. Agnew, Mr. A. Hanid, Miss J. Anguin and Miss I. Jabbal.

I should also like to thank the Ford Foundation whose grant for ecological work within the department has assisted these investigations.

All our work on Mount Kenya was carried out by kind permission of the Director, Mr. Perez Olirido and the Mountain National Park Warden, Bill Woodley.

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