**SWART, JONATHAN MICHAEL**

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# FORAGING BEHAVIOUR OF THE CAPE PANGOLIN *MANIS TEMMINCKII* IN THE SABI SAND WILDTUIN

by

**JONATHAN MICHAEL SWART**

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# FORAGING BEHAVIOUR OF THE CAPE PANGOLIN *MANIS TEMMINCKII* IN THE SABI SAND WILDTUIN

## JONATHAN MICHAEL SWART

**Supervisor:** **Dr. P.R.K Richardson**
Department of Zoology and Entomology
University of Pretoria
Pretoria

## ABSTRACT

Fifteen pangolins were tagged with radio transmitters and their activity, diet, foraging behaviour and habitat selection were studied over a 14 month period in the Sabi Sand Wildtuin. The composition, diversity, and activity of epigaeic ants and termites were also studied concurrently with the pangolin's foraging behaviour.

Twenty-five genera and 55 species of ants and termites were recorded. *Pheidole* sp. 2 was the most common and accounted for 27% of pitfall samples. *Anoplolepis custodiens* contributed to only five percent of the overall species composition, yet it was the predominant prey species in the pangolin's diet. The grassland savanna cleared habitat type had the highest overall species diversity and appeared to be the ideal habitat type for ants. The diversity of ants and termites was greater in summer than in winter for all habitat types. The overall activity of ants and termites was significantly higher during summer than during winter and the activity of *A. custodiens* was 11 times higher during summer compared to winter. Sixty per cent of the total activity of this species was recorded in the calc brack habitat type. The nocturnal activity of ants and termites proved significantly lower than the diurnal activity.

Sub-adults left their dens earlier than adults and pangolins remained active for only approximately four hours a night. There was no significant difference between their winter and summer activity period. Pangolins' preferred temperature range of activity was from 11°C to 25°C and temperature appeared to affect their activity only during winter. Their activity period and feeding intensity was significantly correlated such that the months that their feeding intensity was lower they were active for longer and *vice versa*. Fifteen ant species and five termite species were recorded in the pangolins' diet. The relative importance (RI) of the ants was 96.7% and termites only 3.3%. Six species constituted 97.7% of their diet and the RI of *A. custodiens* was 77.3%. Only 15.7% of the pangolin's foraging time was spent feeding. Feeding bouts averaged only 40 seconds and most feedings (99%) were on prey situated below the soil surface. The remaining 1% were from the soil surface, animal dung and dead twigs. The mean dig depth per feeding bout was only 3.8 cm and ant or termite species that were preyed on from deeper digs were also preyed on for longer and *vice versa*. This also applied to each study animal except the sub-adult pangolin, Imini.

All study animals exhibited a relatively high degree of habitat selectivity. The grassland savanna clearings, mixed tree savanna and calc brack thicket habitat types were selected in preference to the other habitat types whereas pangolins selected against feeding in the marula/*Combretum* sand savanna and riverine thicket habitats. The calc brack thicket habitat type was represented by a mere 3% of the study area yet 42% of the feeding bouts of three pangolins were in this area. Pangolins foraged predominantly on structured soils of the hill slopes. During winter, feeding bouts were distributed evenly between the upper slopes and footslopes of hills, whereas during summer a larger proportion was recorded on the footslopes.

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# CHAPTER 1

# GENERAL INTRODUCTION

Before the appearance of humanity the only real threat to Cape pangolins *Manis temminckii* was from natural predators such as lion. Although a unique covering of sharp imbricated plate-like scales provides them with an effective protection against such predation, it is inadequate as a defence against the toll of increasing human populations.

The status of *M. temminckii* in Southern Africa is considered "threatened" and the reason for this appears threefold. First, pangolin scales are highly sought after by traditional healers for their superstitious value and medicinal properties, and since pangolins are slow moving, they are easily captured and killed. In east Africa all body parts of *M. temminckii* are thought to have some healing property (Mohr 1961). The local demand for pangolins is not clear, however, U.S. import data for 1990 recorded 226 pangolin skins originating in Laos (Anon 1994), and 100 kg of *Manis* spp. scales exported from Madagascar to Korea (Bräutigam, Howes, Humphreys & Hutton 1994).

A second factor that may be a threat to pangolins is the indiscriminant application of pesticides on farmlands. Pangolins are particularly susceptible to chemicals such as Gamma BHC and DDT which have proved fatal to pangolins within 24 hours (Van Ee 1978). In South Africa, *M. temminckii* occurs in the northern Cape Province, western parts of the Orange Free State, northern parts of Natal and western, northern and eastern Transvaal (Smithers 1986). Insecticides are sprayed on farmlands over almost the entire distribution range of pangolins outside protected areas, particularly in the northern Cape Province and the western Orange Free State. They are applied to control locust outbreaks, malaria and crop pests. Even if these poisons do not kill pangolins directly they are likely to affect their food supply by concentrating in their prey, namely: the ants and termites. This may also affect pangolin populations by causing infertility or a general decline in fitness among pangolins, and ultimately extinction within these areas.

Finally, a third factor with a negative effect on pangolin populations is the degradation of natural habitats. In the Eastern Lowveld of South Africa, habitat deterioration is a consequence of deforestation and burning to provide clear areas for human habitation, crops and cattle pastures. In addition many areas are cleared of woody species, which provide wood fuel for domestic use. These practices may result in a decline in the population of ants and termites. Since the occurrence of pangolins appears to be governed by the availability of their ant and termite prey (Smithers 1983), they may be forced to seek new areas with unsuitable habitats for pangolin habitation.

Of the many detailed behavioural ecological studies published on myrmecophagous mammals (e.g., Melton 1976; Lubin & Montgomery 1981; Redford 1983; and Richardson 1987a), few are on pangolin ecology of which none were detailed studies. This may be due to their elusive and nocturnal behaviour or because they occur in relatively low densities when compared to other myrmecophagous mammals. Clearly there is a basic lack of knowledge on aspects required to determine the status of Cape pangolins. Therefore based on the threats facing pangolins the primary motivation for studying their feeding ecology is to establish their basic habitat requirements. Habitat utilisation while feeding, and prey availability in the various habitat types, is of paramount importance in this regard. To determine the habitat requirements and conservation status of *M. temminckii* in the Sabi Sand Wildtuin (SSW) the research was approached with the following objectives:

1) To establish the diversity of ants and termites in the various habitat types and associated soil forms.

2) To establish the daily and seasonal activity of ants and termites to predict their availability as prey.
3) To establish the daily and seasonal activity patterns of pangolins in relation to prey activity.
4) To determine any seasonal variation in the pangolins diet.
5) To determine the relationship between habitat utilisation and diet of pangolins on a seasonal basis.

Numerous mammals exploit the ubiquity of ants and termites as a food source that either supplements or constitutes the bulk of their diet. Approximately 216 mammal species are known to include ants or termites in at least one per cent of their diet and only about 12% of these are obligate myrmecophages with a diet of more than 90% ants or termites (Redford 1987). Pangolins feed exclusively on ants and termites and they have several morphological adaptations that enable them to gain access to the concealed galleries and nests of ants and termites that are inaccessible to most other mammals. Such adaptations include: an acute olfactory sense; a powerful pectoral girdle adapted for digging; a long vermiform tongue for probing the ant or termite galleries; large salivary glands that produce copious amounts of sticky saliva to ensnare the prey; and a muscular pyloric region of the stomach to aid digestion (Sweeney 1956; Kingdon 1971; Smithers 1983).

*M. temminckii* feed on ants and termites close to the soil surface since they are smaller and are less powerful diggers than the larger myrmecophages such as the aardvark *Orycteropus afer* of the drier savanna regions of Africa (Melton 1976); the giant pangolin *Manis gigantea* of the moist equatorial forests of western and central Africa (Kingdon 1971,1984); and the giant armadillo *Priodontes maximus* of South America (Redford 1985b). These larger myrmecophages are all powerful diggers well adapted for digging deep into hard soil. Thus, above gaining access to nests and foraging galleries of the deeper nesting species, they are also able to penetrate the impervious structures constructed by some of the mound building termites such as *Macrotermes* and *Cornitermes*. Cape pangolins occur sympatrically with the larger aardvark but do not dig as deep for their prey. Although they both often prey on the same ant species of the genera *Camponotus* and *Anoplolepis* (Smithers 1983), pangolins appear to feed only on the foraging galleries just beneath the soil surface whereas aardvarks are able to penetrate the nests.

The availability of ant and termite prey close to the soil surface would thus be an important factor in determining the distribution of *M. temminckii.* The availability of ants and termites as prey for pangolins is thus covered in detail in Chapter three. The primary objectives of this part of the study were to determine: (a) whether species preyed on by pangolins were also the most abundant in the study area; and (b) whether the activity and behaviour of these species determined their availability as prey. It is also likely that the activity of certain ant and termite species determine the activity of pangolins. This is evident in the numbat *Myrmecobius fasciatus* which is the only marsupial that is fully diurnal (Friend 1982). This is apparently a consequence of its dependence on termite prey, which are more active in the foraging galleries during the day than at night. In contrast, pangolins are nocturnal which suggests that their prey is more available at night. Pangolin activity is discussed in Chapter four with an attempt to establish the relationship between the activity of pangolins and their prey.

Although several authors have documented some of the feeding habits of *M. temminckii* (see Sweeney 1956, 1973; Kingdon 1971; and Smithers 1983), no emphasis was placed on the frequency that the various prey species were located, the amount of time that pangolins spent feeding on each species and the duration of feeding bouts. This information is important to determine the pangolin's selectivity or preferences for certain prey species and whether pangolins are deterred by the defences of certain ants and termites. A detailed account of their foraging behaviour is given in Chapter 4 with the objective of determining the following: (a) the composition of their diet and whether it reflects a preference for particular species; (b) whether pangolins have a preference for particular castes of ants or termites; (c) whether their foraging behaviour is affected by climatic conditions such as temperature and rainfall; (d) whether the duration of their feeding bouts is reduced by anti-predator defences of ants and termites; and (e) the significance of the variation in the duration of feeding bouts according to the depth that the various prey species are located. A pangolin in the Sabi Sand game reserve, for example, had longer feeding bouts when preying on ant and termite species located deeper in the soil than species closer to the soil surface (Swart 1992). The significance of this behaviour could be important in determining the pangolin's dietary requirements.

Habitat utilisation by pangolins is described in Chapter 5. Until now, very little has been documented on the habitat utilisation of *M. temminckii.* According to Smithers (1983) Cape pangolins occur mainly in savannah woodland but also on floodplain, other grassland areas, rocky slopes and sandveld. This is a very broad description of habitats utilised by pangolins since it refers to their location on a national level. Alternatively, the aim of this research was to establish what their habitat preferences were within a relatively small localised area of approximately 170 km$^2$. In addition, emphasis was placed on areas where pangolins were foraging for ants and termites, in particular the habitat type and their position on the landscape catena. With this information the pangolin’s habitat requirements concerning their feeding behaviour could be determined.

It is intended that the collation of information obtained from this study will provide a better insight into the feeding ecology of pangolins, and hopefully inspire further research on these mammals in other regions.

# CHAPTER 2

# MATERIALS AND METHODS

## INTRODUCTION

This chapter describes the study area and outlines some of the research methods employed during this study, based on the aims of this research and the results of preliminary studies. The study area was chosen because the author was resident in the area and familiar with the terrain. In addition, pangolins were occasionally observed on different locations within this area. Methods of finding pangolins, capturing them, tagging them with radio transmitters and collecting data while following pangolins are described while other methods will be described in the relevant chapters.

## STUDY AREA

### Location and boundaries

The Sabi Sand Wildtuin (SSW) is a fenced privately owned game reserve encompassing an area of approximately 570 km² and situated in the Lowveld of the eastern Transvaal, South Africa. The reserve is located between 24°44'S, 31°19'E (north western corner) and 24°57'S, 31°37'E (south eastern corner) and forms the shape of an inverted "L". The SSW is owned by several proprietors who manage individual "farms" within the total reserve area. The animals are afforded free movement between these properties, however they are restricted from leaving the reserve by an electrified game proof fence. This fence separates a portion of the northern boundary and the entire western boundary from the agricultural lands of Gazankulu, while the western portion of the northern boundary fence separates the reserve from the Manyeleti Game Reserve. Although the SSW was also separated from the Kruger National Park (KNP) on the eastern and southern boundary by a foot and mouth control fence, this was dismantled in July 1993.

The area traversed for research purposes is situated in the north western sector of the SSW and covers an area of approximately 15 000 ha (Fig. 2.1). The farms included in this area are Exeter, Othawa, Wallingford, Ravenscourt, Alicecot and Castleton.

## Physiography and Geology

The topographic position of the reserve lies between the foothills of the Eastern Transvaal great escarpment and the eastern Lowveld plain. The altitude varies from 518 metres above sea level (m.a.s.l.) on Wallingford in the west to 305 m.a.s.l. on Toulon in the south east. The landscape can be described as gently undulating with moderately dissected and rounded hill country, rising between 100 m and 200 m above the floor of the Sand river valley.

The Sand river cuts through the centre of the reserve and is the primary perennial water source in the SSW. It emanates on the Great escarpment above the 1500 m contour and enters the SSW at 400 m.a.s.l. in the North west, flowing for 52 km before leaving the reserve at 270 m.a.s.l. in the South east. The Sabie river, also a perennial river, flows for a distance of 12 km along the southern boundary of the reserve. Most of the tributaries of these two rivers are seasonal. During years of moderate to high rainfall however, pools and springs in several drainage systems may persist well into the dry season.

Most of the reserve is developed on granites and gneisses that belong to the Nelspruit Granite Suite, an acid intrusive volcanic rock (Bristow & Venter 1986). The formation of the granite-gneiss dates back to the Precambrian period approximately 3000 million years before present (B.P.). The Timbavati gabbro,

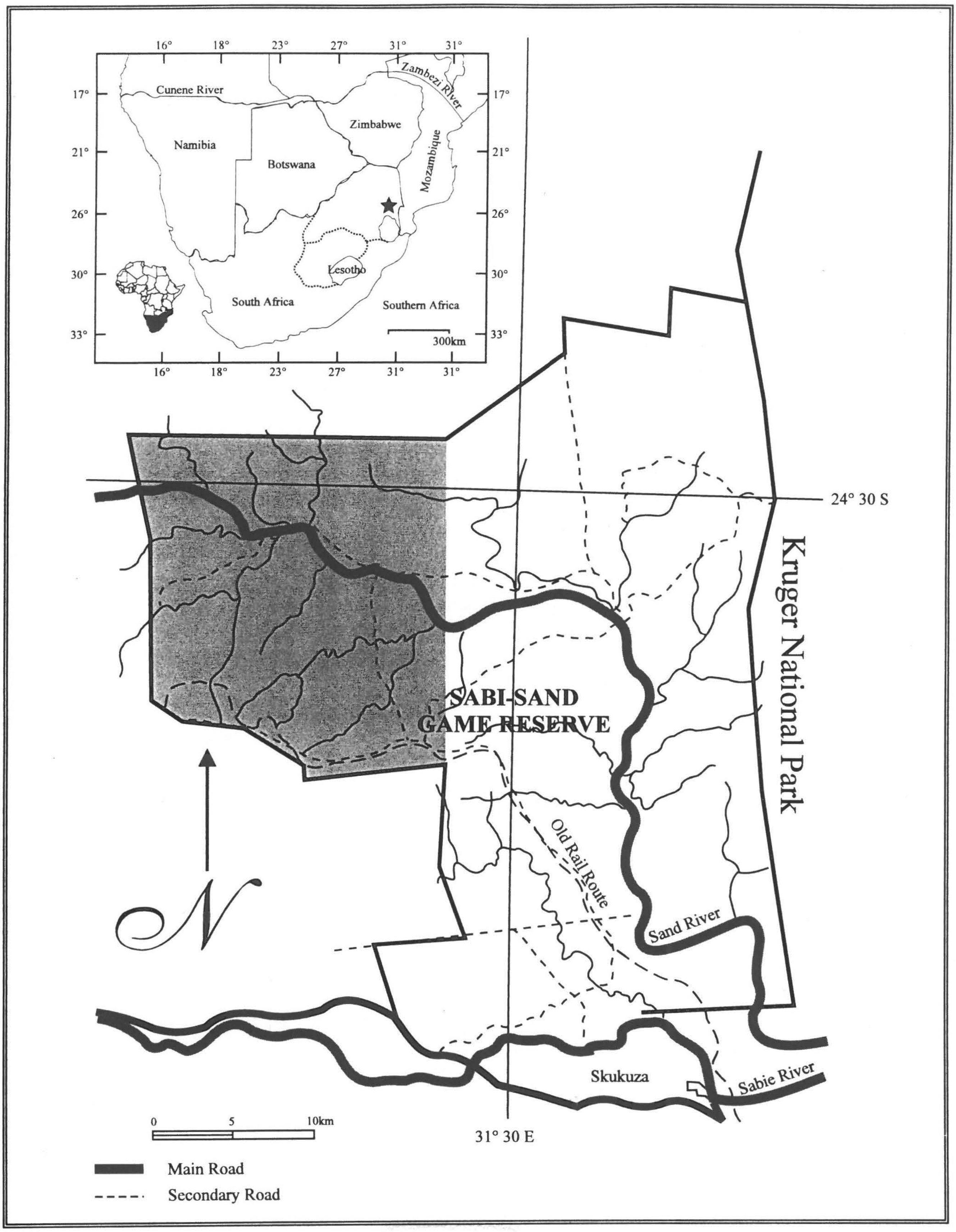


**Fig. 2.1.** Map of the Sabi Sand Wildtuin (game reserve) showing the study area (shaded region) and the postion of the reserve within Southern Africa.

which is composed of several dolerite basic volcanic intrusions dissects this granite-gneiss, forming a grid of dikes and a large sill in the western sector of the reserve (Walraven 1983; Tinley 1979). The intrusion of the Timbavati gabbro through the dikes and sill was partly through Hertzian fractures, which occurred around 1000 m years B.P. (Walraven 1983; Venter & Bristow 1986).

A prominent dolerite dike intrusion, underlying a number of granite topped inselbergs (koppies), extends from east to west across the northern part of the reserve. The inselbergs persisted as a result of locally higher resistance against weathering caused by dome-like structures in the granitoid rocks (Venter & Bristow 1986).

## Soils, vegetation and the landscape catena

The soils of the SSW occur in distinctive catenary sequences on granitoid rocks. Their formation is a result of the following processes: a) the mobilisation and eluviation of clay particles and soluble weathering products from porous soils in upland positions by rain water; b) the lateral downward transportation of these components under the influence of gravitation to footslope positions, where they are redeposited to form impermeable clay horizons. At this point the ground water is forced to the surface, thus forming waterlogged zones (seepage lines) during the rainy season which more or less follow the contours (Venter 1986). Although these catenary sequences associated with granite-gneiss is representative of the area, the presence of gabbro intrusions and dolerite dikes causes a marked change in soil patterns. These metamorphic units generally weather into clayey structured fertile soils which differ from the normal granite-gneiss pattern.

Since climatological and topographical obstructions are absent to the north and north-east of the Lowveld, plants migrate spontaneously into this area resulting in the Lowveld flora bearing a close resemblance to that of tropical Africa (Buitendag 1973). However, since it is situated further south, conditions are not quite as suitable for these tropical plants. Thus, many of the tropical trees do not attain the size they do in tropical Africa and many of the tropical families are not as well represented in the Lowveld.

The vegetation of the study area is broadly classified as Lowveld and arid Lowveld veld types (Acocks veld types 10 & 11 respectively, Acocks 1988). Tinley (1979) divided the vegetation of the SSW into four communities, namely: **aquatic communities** of running water, still water, and acid seepline bogs; **grass communities** including flood plains, contour seeplines, turfs, termitaria, and cleared areas; **savanna communities** including Marula/Combretum sand savannas, knobthorn turf savanna, mixed tree savannas of valley sides, and short thorn savannas; **thicket communities** including riverine areas, calc-brack thicket, and rocky outcrops.

The region falls within the Savanna Biome with a vegetation composition including both moist savanna and arid savanna components (Huntley 1984). The moist savanna component comprises a catena of mesophyllous to microphyllous deciduous woodland and open drainage-line grasslands situated on the crests and upper slopes of hills. Woody species such as *Sclerocarya caffra, Terminalia sericea, Combretum zeyheri, C. collinum,* and *C. apiculatum* dominate the crests. The arid savanna component is physiognomicaly diverse. It includes open sparse grassland with scattered shrubs, tree-base clump formation and short trees to dense thorn thickets where the herbaceous layer may be considerably reduced. The woody components common on the slopes are spinescent microphylls and nanopylls such as *Acacia nigrescens* and *Dichrostachys cinerea,* while *Euclea divinorum* and *Acacia* spp. dominate the foot slopes and catchment areas. A narrow band of riparian vegetation is encountered along the major rivers and drainage lines. The following tree species are common along the banks: *Diospyros mespiliformis; Acacia robusta; Schotia brachypetala; Phoenix reclinata;* and *Ficus sycomorus*.

Thus a general catenary sequence from crest to valley bottom, determined by the sequence of soil complexes (i.e. sandy, hydromorphic, duplex and alluvial) and associated vegetation composition, is repeated regularly across the hills and valleys. This area was the main point of focus during the study of habitat utilisation by pangolins.

## Climate

The SSW falls within an intermediate mesic moisture regime with a unimodal subtropical savanna climate. A single rainy season in summer is generally followed by a single dry season through autumn, winter and spring. The mean rainfall is 570 mm p.a. and the reserve falls within the 550 and 650 isohyets (Gertenbach 1980). The average precipitation in this area occurs in sequences of wet and dry cycles lasting eight to 10 years (Tyson & Dyer 1975, Gertenbach 1980). In general, these cycles are 13% above or below the mean annual rainfall (Gertenbach 1980). For the duration of the research (June 1993 to July 1994) the average rainfall recorded in the study area was 73% of the annual average. The mean monthly rainfall and the mean monthly maximum and minimum temperatures are depicted in Fig. 2.2.

The mean maximum and minimum temperatures recorded at Skukuza weather station during the study were 29.4°C and 13.8°C respectively. The mean daily

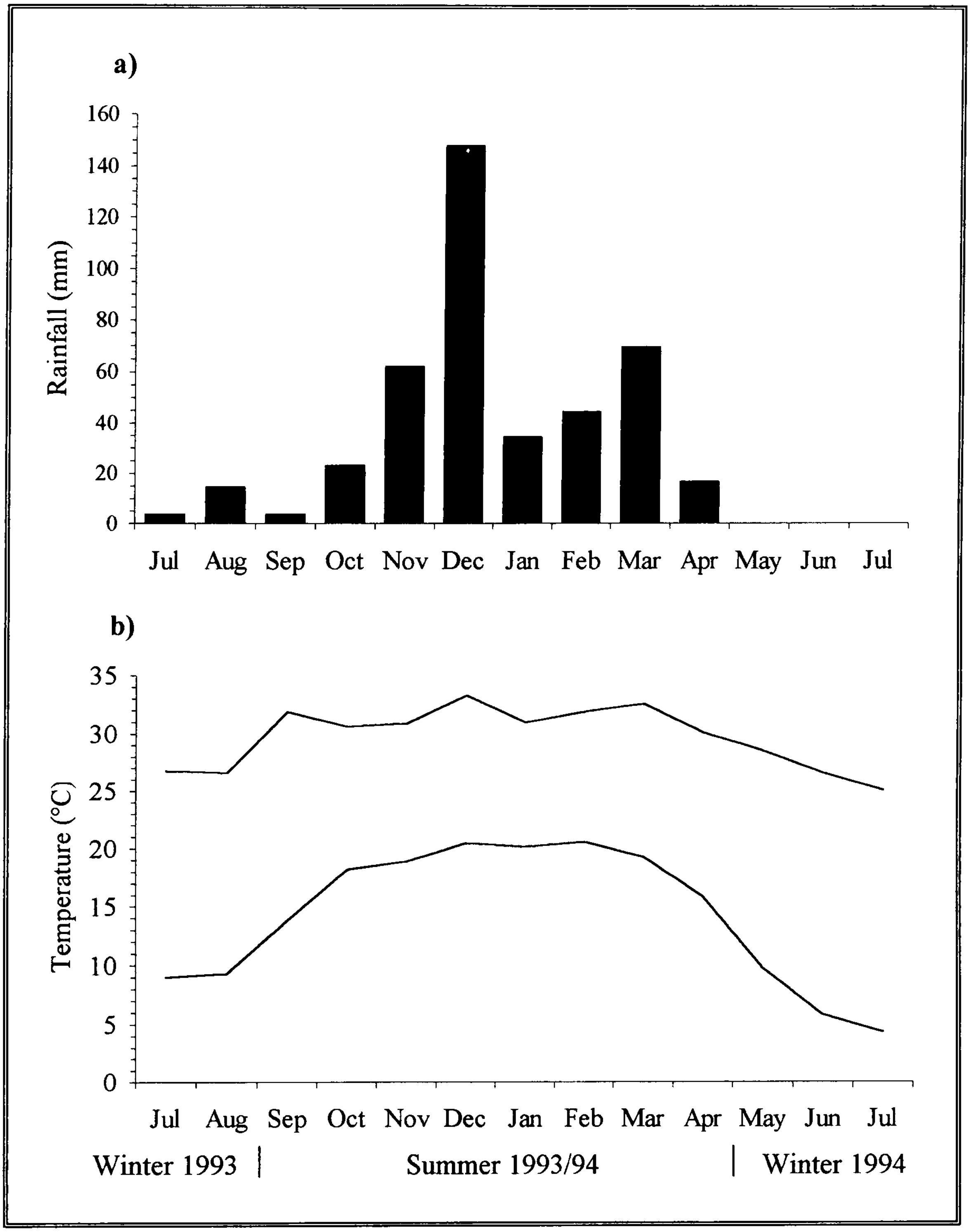


**Fig. 2.2.** The seasonal variation in the mean monthly rainfall (a), and the mean monthly maximum and minimum temperatures (b) for the duration of the study period (July 1993 - July 1994).

maximum and minimum temperatures recorded during summer (September 1993 to April 1994) were 31.5°C and 18.4°C respectively, while the highest recorded temperature was 41.5°C and the lowest 6.2°C. The mean daily maximum and minimum temperatures for winter (June to August 1993 and May to July 1994) were 26.7°C and 7.5°C respectively, reaching a high of 33.6°C and a low of -2.4°C. The temperature along the Sand river and larger drainage systems may be as much as 12°C lower than on the interluve crests. This results from temperature inversion caused by cold air drainage into the valleys at night.

## HABITAT CLASSIFICATION

The habitat types identified for this study were based on the classification of the vegetation of the SSW by Tinley (1979). Panchromatic black-and-white aerial photographs of the study area, photographed during 1985 with a scale of 1:50000 and enlarged to approximately 1:10000, were used to interpret habitat stratification. Areas of homogeneous vegetation were identified on the photographs and each area was then inspected to ensure that they were indeed homogeneous. The nine different habitat types identified in the study area are described below.

### Marula/*Combretum* sand savanna

This habitat type is situated on the crests of the hills and is dominated mainly by mesophyllous woody species such as marula *Sclerocarya birrea caffra*, large-fruited bushwillow *Combretum zeyheri*, weeping bushwillow *Combretum collinum*, red bushwillow *Combretum apiculatum*, silver cluster-leaf *Terminalia sericea*, kiaat *Pterocarpus angolensis*, round-leaved kiaat *Pterocarpus rotundifolius*, green thorn *Balanites maughamii*, buffalo thorn *Ziziphus mucronata*, white raisin *Grewia bicolor* and silver raisin *Grewia monticola*. Woody species that are less common but regarded as key species are wild pear

*Dombeya rotundifolia*, false current resin *Ozoroa insignis*, sourplum *Ximenia caffra*, zebra wood *Delbergia melanoxylon*, spineless monkey orange *Strychnos madagascariensis* and common spike thorn *Maytenus heterophylla*.

The grass species *Panicum maximum* appears to dominate in shaded areas beneath the tree canopies. Other common grass species are *Panicum coloratum, Digitaria eriantha, Melinis repens, Perotis patens, Pogonarthria squarrosa, Eragrostis rigidior* and *Aristida* spp. The grass species *Chloris roxburghiana* and *Cenchrus ciliaris* are often associated with termitaria.

Contour seeplines on the upper slopes below the crests often form the boundary to the marula/*Combretum* habitat type, and in the undisturbed state consist of a narrow band of temporary waterlogged grassland that approximately follows the contours. The key grass species in this zone are *Eragrostis gummiflua, Panicum maximum, Digitaria eriantha* and *Themeda triandra.* However, the majority of contour seeplines have been disturbed by roads and overgrazing that resulted in an encroachment of woody species from above and below the seepline. Large stands of *Terminalia sericea* growing on a seepline is an important indicator of a disturbed seepline. *Combretum zeyheri* also encroaches from the crest onto the seepline, while red thorn *Acacia gerrardii*, common false thorn *Albizia harveyi* and sickle bush *Dichrostachys cinerea*, are common invaders from the slope. Grass species such as *Hyperthelia dissoluta, Aristida meridionalis, Brachiaria nigropedata, Perotis patens, Cynodon dactylon* and *Pogonarthria squarrosa*, are also indicators of a disturbed seepline.

### Grassland savanna clearings

These are areas that have previously been cleared of many of the small trees and shrubs in an attempt to recreate grassland savanna conditions, and are mainly situated along seeplines extending down to the footslopes. Once the contour grassland seeplines were disturbed they were encroached by woody species. This changing vegetation structure pattern where woody vegetation invades open grasslands was termed "bush encroachment" (Strang 1982; West 1947). This prompted several land owners to reclaim those areas that had been subjected to this process by means of a bush clearing program.

Although the soil type and vegetation of these areas are quite variable, the basic vegetation structure is similar in that they are characterised by grassland dotted with shrubs and relatively large trees. The trees and shrubs commonly found in this habitat type are: silver cluster-leaf (on seeplines); marula; zebra wood; knobthorn *Acacia nigrescens*; red bushwillow; leadwood *Combretum imberbe* (on footslopes); weeping wattle *Peltophorum africanum*; buffalo thorn; flaky thorn *Acacia exuvialis*; white raisin; and silver raisin. The more important grass species include: *Aristida congesta*; *Aristida stipitata*; *Panicum maximum* (under tree canopies); *Heteropogon contortus*; *Urochloa mosambicensis*; *Eragrostis rigidior*; *Pogonarthria squarrosa*; *Dactyloctenium* spp; *Digitaria eriantha; Themeda triandra*; and *Eragrostis superba.*

### Mixed tree savanna

These areas are usually situated on the midslope down to the drainage lines and are characterised by a combination of mesophyllous, microphylous and nanophyllous woody species with marula, *Combretum* spp. and *Acacia* spp. dominating. The mixed tree savanna areas are fairly heavily wooded with good grass cover. The more common woody species are marula, weeping bushwillow, red bushwillow, Knobthorn, zebra wood, sickle bush, weeping wattle, round-leaved kiaat, flaky thorn, common spike thorn, red thorn, scented thorn *Acacia nilotica* and *Grewia* spp. Common grass species include *Themeda triandra, Digitaria eriantha, Panicum maximum, Panicum coloratum, Urochloa* *mosambicensis, Eragrostis rigidior, Aristida* spp, *Bothriochloa insculpta* and *Eragrostis superba.*

### Calc brack thicket

These areas are situated on the footslopes on sodic duplex soils close to the Sand river basin. They are characterised by short grass, bush clumps and savanna mosaics. The most important woody species that form bush clumps often associated with termitaria are magic guarri *Euclea divinorum*, tamboti *Spirostachys africana*, lowveld milkberry *Manilkara mochisia*, jacket plum *Pappea capensis*, tree fuschia *Schotia brachypetala*, dwarf boer-bean *Schotia capitata*, common spike thorn, porcupine bush *Dinocanthium hystrix,* kooboo-berry *Cassine aethiopica* and Transvaal saffron *Cassine transvaalensis.* Other trees that often intersperse these bush clumps are knobthorn, scented thorn, red thorn, caterpillar pod *Ormocarpum trichocarpum* and leadwood. The two grass species *Sporobolus nitens* and *Enteropogon monostachyus* appear to dominate in this habitat type with the latter colonising under tree canopies and the former in sunny exposed areas between bush clumps. Other common grasses are *Panicum maximum, Urochloa mosambicensis, Themeda triandra, Digitaria Eriantha, Aristida congesta and Eragrostis superba.*

### Riverine thicket

This habitat type forms a narrow band of riparian vegetation along the major rivers and drainage lines incorporating the Sand river and its major tributaries. Tall trees such as jackal-berry *Diospyros mespiliformis*, sycamore fig *Ficus sycamorus*, tree fuschia, leadwood, matumi *Breonadia salicina*, red ivory *Berchemia zeyheri*, sausage tree *Kigelia africana* and brack thorn *Acacia robusta*, are common along the riverines. Common trees and shrubs that usually form the lower canopies of this habitat are apple-leaf *Lonchocarpus capassa*, black monkey thorn *Acacia burkei*, tamboti, buffalo thorn, russet bushwillow, green thorn, scented thorn, red spike thorn *Maytenus senegalensis*, lavender fever-berry *Croton gratissimus*, fever-berry *Croton megalobotrys*, wild date palm *Phoenix reclinata*, pride-of-De Kaap *Bauhinia galpinii* and potato bush *Phyllanthus reticulatus*.

The dominant grass species of the riverine thicket are *Panicum deustum, Panicum maximum, Cenchrus ciliaris, Eragrostis* spp, *Urochloa mosambicensis* and *Cynodon dactylon.* The reed *Phragmites mauritianus* forms dense stands within the river beds.

### Knobthorn turf savanna

Although this habitat type occurs on red turf and black turf soils the vegetation on both soil types is similar. These areas are essentially dominated by knobthorn trees and white raisin bushes, and the grass species *Themeda triandra* and *Setaria incrassata.* Other woody species such as scented thorn, sickle bush, round-leaved kiaat and magic guarri often form dense thickets in some of these areas. Some of the grasses often associated with these thicket areas are *Aristida* spp, *Eragrostis* spp, *Cymbopogon* spp, *Bothriochloa insculpta* and *Sporobolus nitens.*

### Turf grassland

This is open grassland savanna woodland dominated by trees such as marula, knobthorn, tree wisteria *Bolusanthus speciosus* and apple-leaf. The grass species *Themeda triandra* dominates, however, it may be replaced in some areas by *Cymbopogon* spp. and *Bothriochloa insculpta.* The woody species: sickle bush; round-leaved kiaat; white raisin; red spike thorn; and russet bushwillow also occur in this habitat type, but are usually stunted.

### Riverine floodplain

The large trees found in the riverine thicket areas are absent in the riverine floodplains. These areas are relatively flat and dominated by the wild date palm and lala palm *Hyphaene coriacea*. The woody shrub species are similar to those found in the riverine thicket habitat but their canopy cover is reduced. The grass species of the riverine floodplains are also similar to those found in the riverine thicket.

### Rocky outcrop

The woody species common in this habitat type are marula, cabbage tree *Cussonia spicata*, Transvaal candelabra tree *Euphorbia cooperi*, red bushwillow, knobthorn, common star-chestnut *Sterculia rogersii*, lavender tree *Heteropyxis natalensis* and mountain karee *Rhus leptodictya*. The dominant grass species is *Panicum maximum*.

## STUDY ANIMALS

Since pangolins were extremely difficult to find the land owners and personnel in the reserve were approached to report any animals that were located. A number of commercial Game Lodges, situated in the study area, offer open vehicle photographic safaris to local and overseas tourists. These safaris are usually conducted in the early morning and late afternoon through to the evening until approximately 20h00. If a pangolin was located by one of the safari vehicles, I was informed of its position by radio and the animal was captured. Eleven pangolins were located by safari vehicles, and since they are slow moving animals they are easily captured by hand without the necessity for tranquillising drugs.

An additional method was used to find pangolins. Firstly, a map of the study area was divided into 1km² grids. These grids were subjectively chosen in areas where pangolins were most likely to be found and each grid was divided into ten 100 m wide transects from east to west. Secondly, the transects were walked to record all used and/or abandoned aardvark dens. Thirdly, dens located on these transects were inspected internally with a flashlight and around the entrance for signs of pangolin tracks and faeces. The status of the dens regarding occupancy was then noted and classified as follows: (a) dens occupied by pangolins; (b) dens occupied by other animals; (c) dens suitable for pangolin habitation but not occupied; and (d) dens suitable for pangolin habitation with suspected pangolin occupancy. Finally, if the den was classified as a) or b), an all night watch at the den was carried out on the same day.

Although only two pangolins were located by this method, five additional pangolins were located by following previously located animals. This was usually when animals of the opposite sex found each other.

Once captured, pangolins were tagged with a radio transmitter and released in the same area as found. Translocating or relocating pangolins has never proved successful (Jacobsen *et al.* 1991), and was not attempted. Transmitters and batteries moulded into a dental acrylic unit and shaped to fit onto the posterior dorsal scales was attached to a suitable large scale on the left, mid-region of the tail. Two small holes were hand-drilled into the scale to attach the unit with two 2 mm stainless steel bolts. Two nuts were used on each bolt serving as a lock-nut, and the projecting bolts were sealed with quick-set putty to prevent them from catching onto obstacles.

## Radio tracking and observing pangolins

Once the radio tagged pangolins were released they were not followed on foot for at least a week to ensure that they were not stressed and thus forced to leave the area where they were found. Before any behavioural data could be collected the pangolins had to be habituated to the presence of the observer and flashlight. This was done every night by following them on foot for one hour (or until they showed any sign of being disturbed) from a distance of approximately 10 m. Pangolins lower their ventral surface to the ground and remain motionless when disturbed. Pangolins were usually habituated within one to four weeks although a number of the study animals never became habituated. Once habituated, each animal was followed for the duration of its active period, for one to four consecutive nights. Although it was not always possible to follow them for more than one night, this was done as often as possible to establish whether they foraged in the same area on consecutive nights.

Each evening was begun by driving out by vehicle at around sunset to locate a pangolin. A Yaesu 2m, model FT-290R II radio receiver and a hand held two element yagi antenna were used for tracking the study animals. Pangolins were initially tracked from the vehicle by road. Once the closest perpendicular point between the road and the pangolin was reached, tracking was continued on foot until the pangolin was located.

When the position of the pangolin's den was known, the evening observation began by waiting a distance of approximately 100 metres from the den until the pangolin emerged. The animal was then followed on foot until it returned to a den. The pangolin was tracked on foot only once it was further than 100 m from the den. Thereafter it was tracked to within hearing distance, since they usually move somewhat noisily through the undergrowth and can be heard from a distance of approximately 30 m. The pangolin was then approached slowly and quietly until within five to 10 metres, when it was clearly visible. If this initial approach was not attempted cautiously and the animals were disturbed, they appeared to remain sensitive to the observer's presence for the remainder of the evening, resulting in observer bias.

Observations were made on foot and animals were followed quietly and observed with a flashlight from a distance of approximately 10 metres. All observations were recorded on a data sheet while the pangolin moved between feeding sites. The method of data collection chosen for this study was a combination of focal sampling and continuous recording (Martin & Bateson 1986). That is, one animal was focused on at a time for a specified period of time (focal sampling), while data was recorded continuously so that true frequencies, durations and times at which behaviour patterns started and stopped were measured. This method was chosen since pangolins are solitary, slow moving animals that can be approached to within a few metres, thus permitting detailed data collection.

The time, temperature, habitat type, soil type and the animal's activity were noted with every data record. These parameters were recorded with every feeding and at 50 m intervals if feedings were farther than 50 m apart. Thus the number of records per evening depended on the number of times that pangolins fed and how far they moved. The habitat and soil types where the pangolins foraged were recorded to test whether habitat selection was correlated with prey species abundance and diversity.

# CHAPTER 3

# COMPOSITION, DIVERSITY AND ACTIVITY OF EPIGAEIC ANTS AND TERMITES

## INTRODUCTION

Although several studies were conducted on ants in the eastern Lowveld, they all focused on the symbiosis between certain species of ants and honeydew-producing Homoptera, and the control of these ants in citrus orchards (see Samways 1981; Samways, Nel & Prins 1982; Samways 1983). This is the first study on ant ecology in the Sabi Sand Wildtuin and this chapter describes the species composition, richness, dominance, diversity and activity of the epigaeic ant and termite fauna of this area. Although termites were considered in this study more emphasis was placed on ant populations.

Several studies have revealed that the species composition of ants is strongly influenced by vegetation (Ashton 1979; Greenslade 1971; Greenslade & Greenslade 1977; Anderson 1983). Other studies have shown that ant communities undergo pronounced seasonal changes and that several species exhibit distinctive diel patterns of foraging activity (Briese & Macauley 1980; Greenslade 1979). Thus, the ant composition of different sites representing different habitat types are compared and the seasonal and diel activity of the component species is examined. This research was done in order to establish the seasonal availability of prey for pangolins within the different habitat types.

## METHODS

### Sampling

Seasonal diversity, abundance and activity of prey species were determined with the aid of pitfall traps. Pitfall traps are a useful method for indicating species distribution preferences (Greenslade 1964), for monitoring populations (Luff 1975), determining species richness in various habitats (Samways 1983; Marsh 1986), assessing relative population levels (Baars 1979; Jennings, Hauseweart & Dunn 1986) and interhabitat comparisons (Marsh 1984).

The pitfall structure was modified from Majer (1978). Traps consisted of an outer case of a 160 mm length of hard plastic tubing of 20 mm internal diameter sunk into the ground, and containing a rimmed Pyrex test tube (145 mm deep, 16 mm internal diameter). A 40 mm depth of soap-water solution was placed in each tube to act as a surfactant preventing the ants or termites from escaping.

Although nine habitat types were identified in the study area, pitfall traps were inserted only in the five habitat types that were representative of the areas where pangolins were located (see Chapter 2 for a description of the habitat types). Twelve pitfall traps were inserted into the ground in each of the following five habitat types: (i) marula/*Combretum* sand savanna (MC); (ii) mixed tree savanna (MT); (iii) grassland savanna clearings (GC); (iv) calc brack thicket (CB); and (v) riverine thicket (RT). Each habitat type was represented by a 30m x 40m sample site that was divided into twelve 100m$^2$ quadrats. One pitfall trap was placed approximately in the centre of each of the twelve 10m x 10m quadrats within each sample site. Six were placed in shaded areas and six in the open exposed to sunlight. This method, suggested by L.E.O. Braak (pers. comm., Kruger National Park, Skukuza), was used to ensure that ant and termite activity was sampled in both shaded and exposed areas. Thus a total of 60 pitfall traps were used to sample all five habitat types.

The catches immediately after a pitfall trap is placed in position are commonly found to be higher than those subsequently achieved (Joosse (1965) and Greenslade (1973) termed these "digging-in" effects). This effect was accommodated for by first sampling the pitfall traps two weeks after insertion. Thereafter the pitfall traps were inserted for 24 hours every week and checked at dawn and dusk from July 1993 to July 1994. By identifying and counting the number of species after each catch, an estimate of diel and seasonal activity of ants and termites was determined.

**Data analysis**

Since ants and termites live in colonies, individuals are usually not evenly distributed and the number collected in pitfall traps per species per sample is also not a normal distribution. In addition, the probabilities of collecting individuals of the same species at a given spot are not independent. Thus parametric statistics are generally inappropriate, and nonparametric statistics were used for most comparisons.

The following parameters were defined for the measurement of species contributions to overall diversity:

a) Species richness (per sample site) = the total number of species identified at any pitfall trap in the sample site during the course of the entire sample period.

b) Total activity = $\sum p_i$ where $p_i$ = the proportion of pitfall sample checks in the sample site where species $i$ was found.

c) The Shannon-Wiener function, $H' = -\sum p_i \ln p_i$ (Shannon & Weaver, 1949) where $H'$ = diversity and $p$ = the proportion of pitfall checks within a sample site comprising the *i*th species.

d) $J = H'/H_{max}$ where $J$ = evenness of species occurrence within a sample site and $H_{max} = \ln S$ where $S$ = the number of species per sample site.

e) Berger-Parker dominance index, $d = N_{max}/N_T$ (Berger & Parker, 1970) where $N_{max}$ = the number of pitfall sample checks where the dominant species was recorded and $N_T$ = the total number of pitfall sample checks where any species was recorded. For reasonable values of $S$ the index is not influenced by the total number of species (Southwood, 1978).

Several methods for the measurement of species diversity have been suggested, however the Shannon-Wiener function (Shannon & Weaver, 1949) is most frequently used in ant community studies. The relative merits and drawbacks of $H'$ are discussed by Hurlbert (1971) and Whittaker (1972). It is applied in the present study only as a comparative measure, since its value *per se* is biologically meaningless. For a given number of species $H'$ is maximised when individuals are distributed equally amongst species, thus it is preferable to have some measure of the evenness of species distribution. This was achieved by applying the evenness index *(J)* proposed by Pielou (1966) to aid the interpretation of $H'$. $J$ is the percent of maximum $H'$ that is found at each site and standardises $H'$ for differences in species number between pitfall traps.

Thus, to compare ant communities, the four parameters; species richness, overall diversity as measured by $H'$, the evenness of distribution, and the dominance index; were used to ensure the clearest possible interpretation of diversity differences.

# RESULTS

## Composition of the ant and termite fauna

Pitfall trapping proved successful as a method for sampling the epigaeic ant and termite fauna, whence a total of 27 067 individuals from 5 449 records representing 25 genera and 55 species were recorded (Table 3.1). The Formicidae were represented by 20 genera and 50 species while only five genera and five species of termites were recorded.

A total of 6480 pitfall sample checks was carried out over 54 days, during the period July 1993 to July 1994. The cumulative species curve, shown in Fig. 3.1, has a reasonably constant positive slope for the first 45 sampling periods while new species were encountered. However, a slight flattening of the curve from the 45th sampling period indicates that it is likely that the majority of epigaeic species were sampled during this period. This is also indicated by the columns in fig 3.1 showing that only a few new species were recorded between the 45th and 54th sampling period. However, it can not confidently be claimed that the faunal list of Table 3.1 is complete since many subterranean and arboreal species were not sampled. In addition, the sporadic occurrence of rarer species due to the periodicity of seasonal activity requires several seasons of sampling to include these species.

The abundance ($N_2$), which is the number of individuals of each ant and termite species sampled in pitfall traps, and the frequency of occurrence ($N_1$), which is the number of pitfall sample checks where each species was found, is given in table 3.1. The closer the value of ($N_1$) is to ($N_2$) the more evenly a species is distributed. From Table 3.1 it is apparent that the abundance figures ($N_2$) are somewhat misleading since they do not give a clear indication of the

**Table 3.1.** The frequency of occurrence ($N_1$) and the abundance ($N_2$) of each species of epigaeic ant and termite sampled with pitfall traps at five different sites during the period July 1993 to July 1994. Each site represents a different habitat type as follows: MC = Marula/*Combretum* sand savanna; GC = Grassland savanna clearings; MT = Mixed tree savanna; CB = Calc brack thicket; RT = Riverine thicket.

| | MC | | GC | | MT | | CB | | RT | | TOTAL | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANT AND TERMITE SPECIES | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ |
| **FORMICIDAE** | | | | | | | | | | | | |
| **Aenictinae** | | | | | | | | | | | | |
| *Aenictus eugenii* Emery | 1 | 1 | | | 4 | 6 | 1 | 1 | 1 | 1 | 7 | 9 |
| **Dolichoderinae** | | | | | | | | | | | | |
| *Tapinoma* sp. 1 | 12 | 12 | 2 | 2 | | | | | 1 | 2 | 15 | 16 |
| *Tapinoma* sp. 2 | 7 | 12 | 2 | 2 | | | | | | | 9 | 14 |
| *Technomyrmex albipes* (Smith) | 31 | 62 | 11 | 12 | 7 | 24 | 16 | 21 | 67 | 186 | 132 | 305 |
| **Formicinae** | | | | | | | | | | | | |
| *Anoplolepis* sp. 1 | | | 2 | 7 | | | | | | | 2 | 7 |
| *Anoplolepis custodiens* (Smith) | 33 | 415 | 3 | 3 | 50 | 1065 | 183 | 6576 | 5 | 68 | 274 | 8127 |
| *Camponotus* sp.- *maculatus* -group | 1 | 1 | 2 | 2 | | | 1 | 1 | | | 4 | 4 |
| *Camponotus cinctellus* (Gerstaecker) | 1 | 1 | | | | | 1 | 1 | 1 | 1 | 3 | 3 |
| *Camponotus congolensis* Emery | 1 | 1 | 3 | 3 | | | 1 | 1 | 1 | 1 | 6 | 6 |
| *Lepisiota capensis* (Mayr) | | | 1 | 1 | 2 | 2 | 3 | 3 | 49 | 85 | 55 | 91 |
| *Lepisiota spinosior* (Forel) | | | 7 | 7 | | | 3 | 3 | 4 | 5 | 14 | 15 |
| *Lepisiota submetallica* Arnold | 10 | 10 | 10 | 10 | 24 | 36 | 2 | 2 | 37 | 59 | 83 | 117 |
| *Plagiolepis* sp. 1 | 6 | 6 | 7 | 8 | 7 | 9 | 7 | 10 | 13 | 49 | 40 | 82 |
| *Plagiolepis* sp. 2 | | | 1 | 1 | | | | | | | 1 | 1 |
| *Polyrhachis schistacea* (Gerstaecker) | 1 | 1 | 3 | 3 | | | 1 | 1 | | | 5 | 5 |
| **Myrmicinae** | | | | | | | | | | | | |
| *Crematogaster* sp. 1 | 1 | 1 | | | 1 | 1 | 3 | 4 | 33 | 133 | 38 | 139 |
| *Crematogaster* sp. 2 | 4 | 6 | | | | | | | | | 4 | 6 |
| *Crematogaster* sp.- *castanea* -group | 10 | 13 | 19 | 78 | 24 | 79 | 46 | 133 | 26 | 111 | 125 | 414 |
| *Melissotarsus beccarii* Emery | | | | | 1 | 1 | | | | | 1 | 1 |

**Table 3.1 cont.**

| ANT AND TERMITE SPECIES | MC | | GC | | MT | | CB | | RT | | TOTAL | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ |
| *Meranoplus inermis* Emery | 1 | 1 | | | | | | | | | 1 | 1 |
| *Meranoplus magrettii* André | 1 | 1 | 4 | 4 | | | 5 | 5 | | | 10 | 10 |
| *Meranoplus nanus* André | | | | | | | | | 1 | 1 | 1 | 1 |
| *Meranoplus sthenus* Bolton | 3 | 3 | | | 1 | 1 | | | | | 4 | 4 |
| *Monomorium damarense* Forel | 309 | 1002 | 340 | 812 | 280 | 639 | 215 | 306 | 129 | 254 | 1273 | 3013 |
| *Monomorium emeryi* Mayr | 13 | 18 | 1 | 1 | | | | | 1 | 1 | 15 | 20 |
| *Monomorium havilandi* Forel | | | 1 | 1 | | | 1 | 1 | | | 2 | 2 |
| *Monomorium junodi* Forel | 58 | 249 | 188 | 2045 | 111 | 345 | 167 | 521 | 45 | 90 | 569 | 3250 |
| *Monomorium mictilis* Forel | 18 | 235 | 12 | 43 | 2 | 2 | 3 | 6 | 5 | 36 | 40 | 322 |
| *Monomorium* sp.- *mediocre* -complex | 4 | 22 | 1 | 1 | 2 | 6 | 1 | 1 | | | 8 | 30 |
| *Myrmicaria natalensis* (Mayr) | 2 | 2 | 22 | 69 | 1 | 1 | 2 | 2 | 12 | 21 | 39 | 95 |
| *Ocymyrmex fortior* Santschi | 65 | 121 | 41 | 65 | 34 | 47 | 14 | 21 | 20 | 24 | 174 | 278 |
| *Pheidole* sp. 1 | 1 | 1 | 1 | 1 | | | | | 3 | 3 | 5 | 5 |
| *Pheidole* sp. 2 | 332 | 1934 | 361 | 1945 | 307 | 1197 | 134 | 1140 | 364 | 2354 | 1498 | 8570 |
| *Pheidole* sp. 3 | 2 | 2 | | | 2 | 4 | | | 18 | 33 | 22 | 39 |
| *Pheidole* sp. 4 | | | | | | | | | 8 | 12 | 8 | 12 |
| *Solenopsis* sp. 1 | | | 1 | 1 | | | 5 | 27 | 6 | 13 | 12 | 41 |
| *Tetramorium constanciae* Arnold | | | | | | | 2 | 10 | | | 2 | 10 |
| *Tetramorium do* Forel | 14 | 16 | 30 | 35 | 18 | 18 | 17 | 18 | 42 | 54 | 121 | 141 |
| *Tetramorium inezulae* (Forel) | 59 | 248 | 2 | 2 | 2 | 3 | | | 5 | 5 | 68 | 258 |
| *Tetramorium longicorne* Forel | | | | | | | 1 | 1 | 1 | 1 | 2 | 2 |
| *Tetramorium mossamedense* Forel | | | 2 | 2 | | | | | 1 | 1 | 3 | 3 |
| *Tetramorium notiale* Bolton | | | 4 | 5 | | | | | 2 | 2 | 6 | 7 |
| *Tetramorium oculatum* Forel | 1 | 1 | | | | | | | | | 1 | 1 |
| *Tetramorium sericeiventre* Emery | 61 | 81 | 123 | 207 | 36 | 86 | 18 | 24 | 28 | 37 | 266 | 435 |
| *Tetramorium setigerum* Mayr | 2 | 2 | 15 | 18 | 1 | 1 | 2 | 2 | 22 | 27 | 42 | 50 |
| *Tetramorium setuliferum* Emery | 11 | 16 | 19 | 161 | 1 | 1 | 5 | 7 | | | 36 | 185 |

**Table 3.1 cont.**

| ANT AND TERMITE SPECIES | MC | | GC | | MT | | CB | | RT | | TOTAL | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ | $N_1$ | $N_2$ |
| *Tetramorium* sp.- *oculatum* -complex | 96 | 159 | 82 | 129 | 40 | 52 | 9 | 24 | 15 | 22 | 242 | 386 |
| **Ponerinae** | | | | | | | | | | | | |
| *Odontomachus troglodytes* Santschi | 16 | 20 | 13 | 14 | 23 | 27 | 3 | 3 | 8 | 8 | 63 | 72 |
| *Pachycondyla kruegeri* Forel | 2 | 2 | 1 | 1 | 3 | 3 | 4 | 4 | 24 | 25 | 34 | 35 |
| *Plectroctena mandibularis* Smith | 1 | 1 | | | | | 1 | 1 | 1 | 1 | 3 | 3 |
| **TERMITIDAE** | | | | | | | | | | | | |
| Termitidae (unidentified sp.) | 6 | 9 | 4 | 4 | 4 | 5 | 2 | 4 | | | 16 | 22 |
| **Hodotermitidae** | | | | | | | | | | | | |
| *Hodotermes mossambicus* Hagen | 1 | 1 | 5 | 198 | 2 | 2 | 9 | 28 | 1 | 1 | 18 | 230 |
| **Macrotermitinae** | | | | | | | | | | | | |
| *Macrotermes falciger* Gerstäcker | 1 | 27 | | | | | | | | | 1 | 27 |
| *Odontotermes* sp. | 1 | 2 | 4 | 4 | 5 | 6 | 4 | 7 | 2 | 2 | 16 | 21 |
| **Nasutitermitinae** | | | | | | | | | | | | |
| *Rhadinotermes coarctatus* Sjöstedt | 1 | 30 | 5 | 86 | | | | | | | 6 | 116 |
| *Trinervitermes trinervoides* Sjöstedt | | | 2 | 5 | 2 | 3 | | | | | 4 | 8 |
| TOTALS | 1201 | 4748 | 1357 | 5998 | 997 | 3672 | 892 | 8920 | 1002 | 3729 | 5449 | 7067 |
| TOTAL NUMBER OF SPECIES | 42 | | 41 | | 30 | | 36 | | 37 | | 55 | |

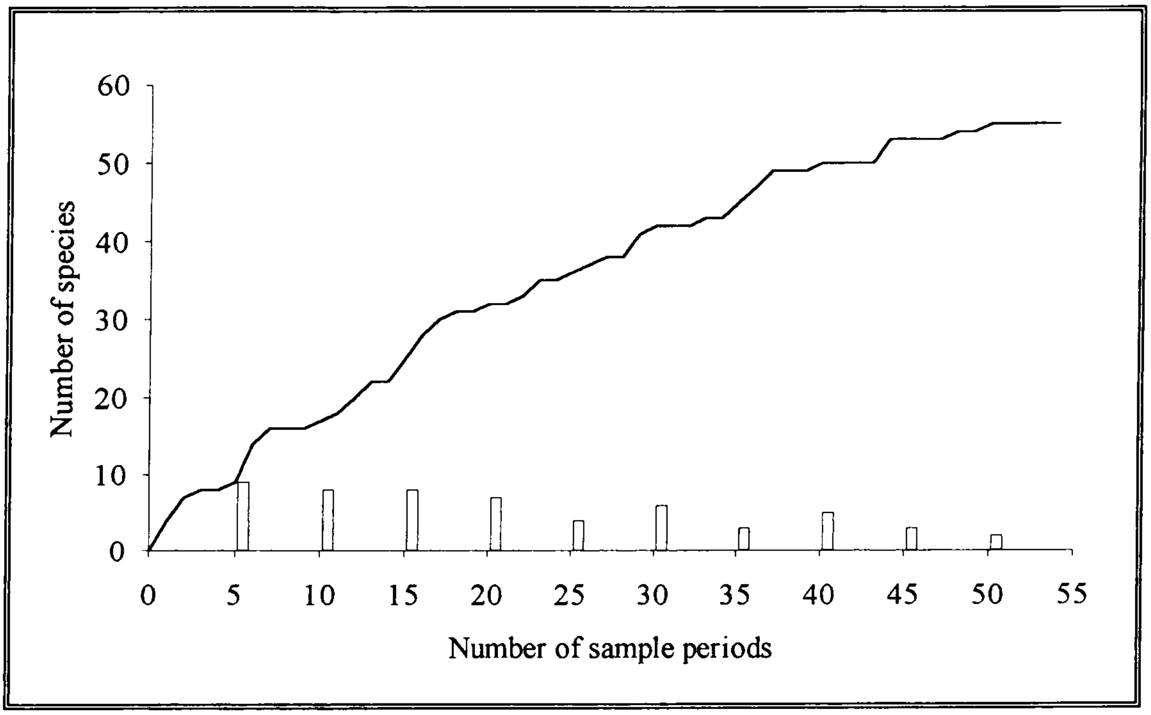


**Fig. 3.1** Cumulative species curve for ants and termites collected during 54 separate 24-hour sample periods. The columns represent the number of additional species trapped after every fifth sample period.

composition, activity, diversity, and distribution of these species in the various habitats. This is evident in the species *A. custodiens*, which were often trapped in large numbers within a single sample. This resulted in a large emphasis being placed on species recorded in fewer samples, yet high in abundance (Table 3.1).

The percent contribution of the 10 most dominant species to each habitat type during winter and summer is given in table 3.2. To compensate for the emphasis on high abundance values, calculations were based on the number of times each species was caught in a pitfall trap. Four species of ants accounted for 65% of the total pitfall catches. Of these the most common species was *Pheidole* sp. 2 which contributed to 27% of occurrences, while *M. damarense* accounted for 23%, *M. junodi* 10%, and *A. custodiens* 5%.

Of the 55 species sampled in pitfall traps 34% were common to all habitat types, while 14% were recorded in four of the five habitat types, 20% in three habitat types, 14% in two habitat types, and the remaining 18% in only one habitat type (Table 3.1). Thus, for some species there appears to be a marked habitat preference, however all species that were sampled in only one habitat type occurred in low numbers, suggesting that they may be rare species sampled by chance.

The overall species composition of each habitat type is illustrated in Fig. 3.2. The two species *M. damarense* and *Pheidole* sp. 2 occurred in more than 50% of pitfall samples in each habitat type, except the calc brack thicket (CB) site, where *A. custodiens* and *M. junodi* also occurred frequently. The first two species accounted for 38% of catches in the CB site while the latter two species contributed to 21% and 19% respectively (Fig. 3.2). *A. custodiens* displayed marked habitat preference, since it occurred at least four fold more frequently in this site than in the other four sites.

**Table 3.2.** The percent contribution of the 10 most abundant species to each habitat type during winter (W) and summer (S). Figures represent the number of times each species was caught in a pitfall trap, and expressed as a percentage of the total number of records in each habitat.

| | MC | | GC | | MT | | CB | | RT | | TOTAL | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ANT AND TERMITE SPECIES | W | S | W | S | W | S | W | S | W | S | W | S |
| *Pheidole* sp. 2 | 25.5 | 28.9 | 28.4 | 26.0 | 27.8 | 31.9 | 12.3 | 15.7 | 38.4 | 35.1 | 28.1 | 27.2 |
| *Monomorium damarense* | 26.9 | 25.1 | 27.8 | 24.1 | 42.5 | 22.7 | 44.7 | 18.9 | 11.2 | 13.9 | 28.0 | 21.4 |
| *Monomorium junodi* | 2.9 | 5.9 | 12.4 | 14.3 | 6.6 | 12.8 | 15.6 | 19.5 | 4.2 | 4.7 | 7.2 | 11.8 |
| *Anoplolepis custodiens* | 2.0 | 3.2 | | 0.3 | 0.4 | 6.8 | 6.7 | 24.0 | | 0.8 | 1.4 | 6.6 |
| *Tetramorium sericeiventre* | 3.8 | 5.8 | 5.6 | 10.2 | 1.5 | 4.4 | 1.7 | 2.1 | 1.8 | 3.4 | 3.1 | 5.6 |
| *Tetramorium* sp.- *oculatum* -complex | 10.2 | 6.7 | 6.2 | 6.0 | 5.1 | 3.6 | 1.7 | 0.8 | 2.9 | 0.6 | 5.8 | 3.9 |
| *Ocymyrmex fortior* | 1.1 | 7.9 | 1.8 | 3.4 | 0.4 | 4.6 | | 2.0 | | 3.2 | 0.7 | 4.2 |
| *Technomyrmex albipes* | 0.7 | 3.7 | 1.2 | 0.7 | 1.5 | 0.4 | 6.7 | 0.6 | 11.5 | 3.7 | 4.1 | 1.7 |
| *Crematogaster* sp.- *castanea* -group | 1.1 | 0.7 | 2.7 | 1.0 | 1.8 | 2.6 | 3.9 | 5.5 | 3.7 | 1.9 | 2.5 | 2.2 |
| *Tetramorium do* | 1.6 | 0.9 | 2.1 | 2.3 | 2.9 | 1.4 | 1.1 | 2.1 | 2.3 | 5.3 | 2.0 | 2.3 |
| All other species | 24.2 | 11.2 | 11.8 | 11.7 | 9.5 | 8.8 | 5.6 | 8.8 | 24.0 | 27.3 | 17.0 | 13.0 |

MC = Marula/Combretum sand savanna; GC = Grassland savanna clearings; MT = Mixed tree savanna; CB = Calc brack thicket; RT = Riverine thicket.

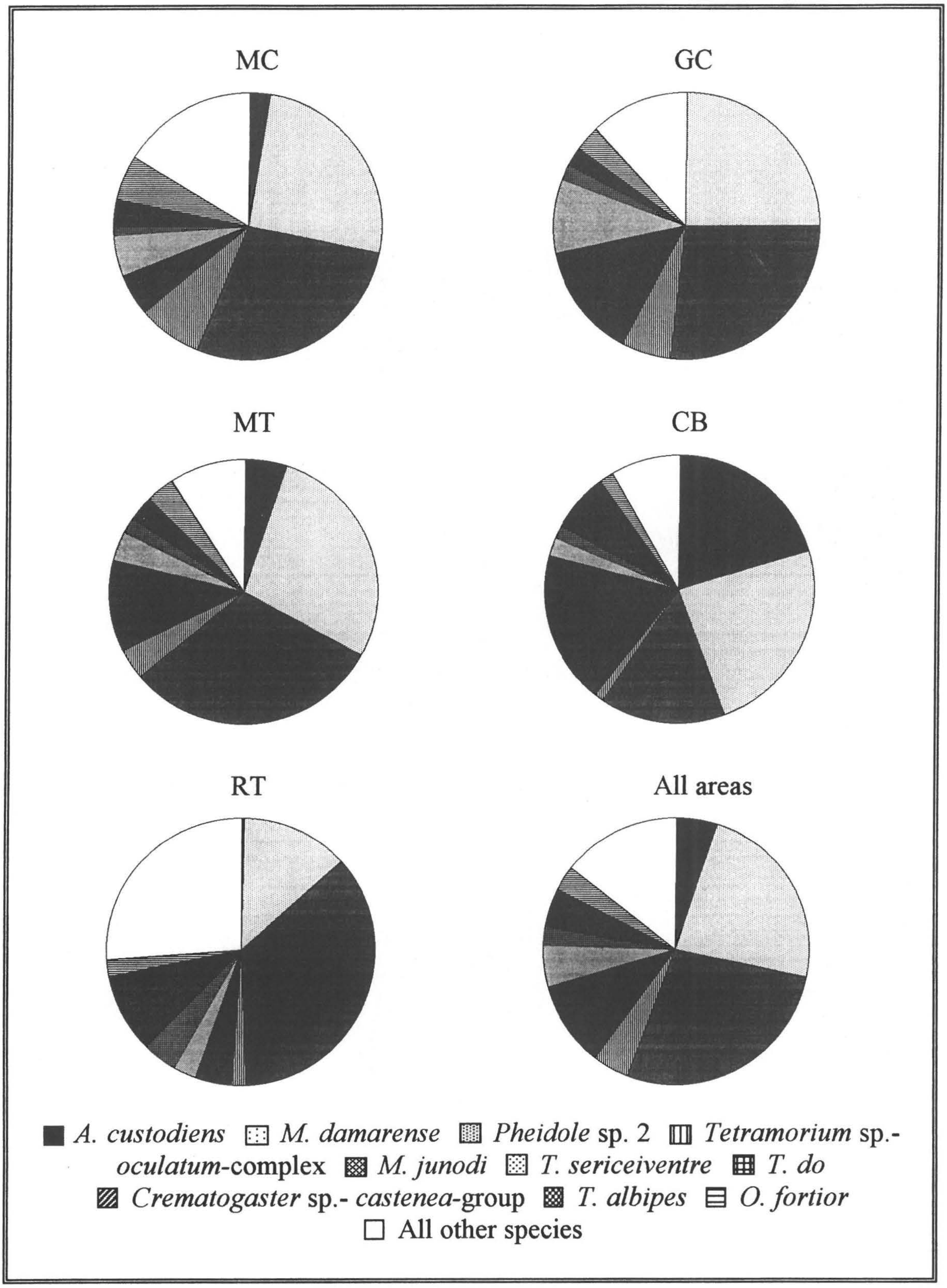


**Fig. 3.2** Species composition of each habitat type as recorded in pitfall traps. Species caught in more than 100 samples are illustrated.

Interestingly, *A. custodiens* contributed to only five percent of the overall species composition (Fig. 3.2), yet it is the predominant prey species in the pangolin's diet (see Chapter 4). However, when *A. custodiens* was compared with other species of the same size or larger (i.e. larger than 0.5 cm), its overall contribution was 43% (Fig. 3.3). This comparison resulted in *A. custodiens* being most abundant in the calc brack site and the mixed tree site where its contribution was 84% and 44% respectively (Fig. 3.3). The ant species *O. fortior* was the second most common species of the larger species, making up 28% of the overall composition (Fig. 3.3).

**Species diversity**

Several indices used for the measurement of species diversity in the various habitats, during winter and summer, are given in Table 3.3. The grassland savanna site had the highest overall diversity ($H' = 2.32$), followed by the marula/*Combretum* site ($H' = 2.26$), the riverine thicket site ($H' = 2.11$), and the mixed tree site ($H' = 1.82$). The lowest overall diversity was recorded in the calc brack site ($H' = 1.78$). For all habitat types a higher diversity index ($H'$) was accompanied by a greater evenness of distribution ($J'$), ($r = 0.98$; $df = 3$; $p < 0.01$).

The diversity ($H'$) of the ant and termite faunas were greater in summer than in winter for all habitat types (Table 3.3; Fig. 3.4). Their evenness of distribution was also higher during summer in all bar the marula/*Combretum* habitat type (Table 3.3). During summer the grassland savanna (GC) site had the highest diversity, whereas during winter the marula/*Combretum* (MC) site was the highest (Fig. 3.4). Interestingly, the coefficient of variance in diversity ($H'$) between the various habitats of 9% during summer was considerably lower than the 28% recorded during winter. In addition, the diversity of the

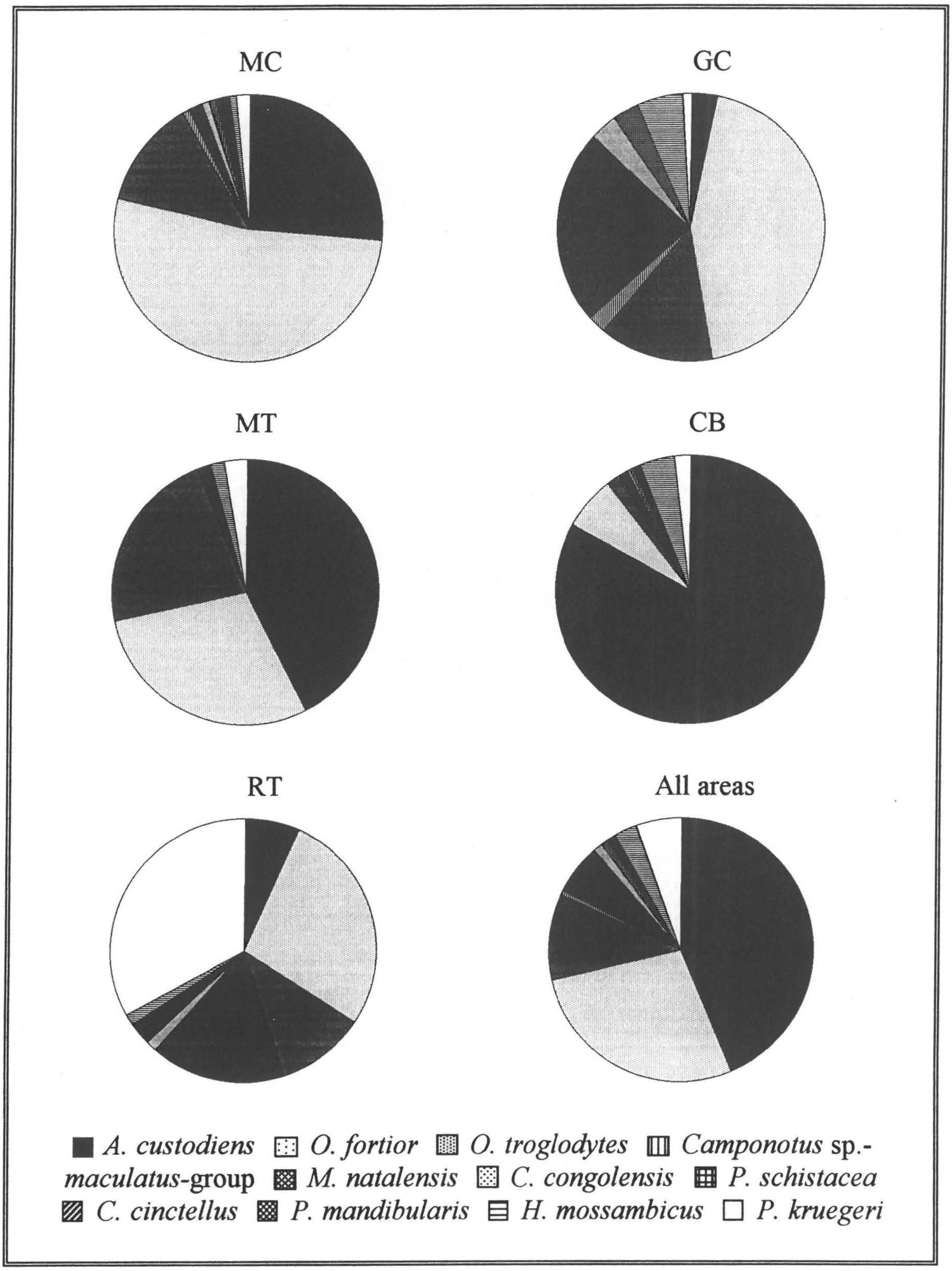


**Fig. 3.3.** Species composition of each habitat type for all species larger than 0.5 cm long that was recorded in pitfall traps.

**Table 3.3.** Seasonal differences in the indices used for measuring the diversity of ants and termites caught in pitfall traps during winter (W) and summer (S).

| | $H'$ | | $J'$ | | $d$ | | $S$ | | $N$ | |
|---|---|---|---|---|---|---|---|---|---|---|
| | S | W | S | W | S | W | S | W | S | W |
| **Habitat** | | | | | | | | | | |
| MC | 2.260 | 2.094 | 0.631 | 0.643 | 28.9% | 26.9% | 36 | 26 | 758 | 443 |
| GC | 2.595 | 1.667 | 0.749 | 0.506 | 26.0% | 28.4% | 32 | 27 | 1019 | 338 |
| MT | 2.053 | 1.292 | 0.638 | 0.412 | 31.9% | 42.5% | 25 | 23 | 724 | 273 |
| CB | 2.122 | 0.987 | 0.602 | 0.374 | 24.0% | 44.7% | 34 | 14 | 713 | 179 |
| RT | 2.174 | 1.842 | 0.622 | 0.587 | 35.1% | 38.4% | 33 | 23 | 619 | 383 |
| **Location** | | | | | | | | | | |
| Exposed | 2.678 | 1.695 | 0.708 | 0.481 | 22.2% | 31.1% | 44 | 34 | 2203 | 788 |
| Shade | 2.108 | 1.739 | 0.561 | 0.489 | 34.8% | 32.1% | 43 | 35 | 1630 | 828 |
| **Activity** | | | | | | | | | | |
| Nocturnal | 2.029 | 1.396 | 0.533 | 0.415 | 40.0% | 34.8% | 45 | 29 | 1604 | 686 |
| Diurnal | 2.608 | 1.910 | 0.681 | 0.537 | 22.1% | 29.4% | 46 | 35 | 2229 | 930 |
| **TOTALS** | 2.447 | 1.744 | 0.622 | 0.470 | 27.2% | 28.1% | 51 | 41 | 3833 | 1616 |

$H'$ = Shannon-Wiener diversity index; $J'$ = evenness; $d$ = Berger-Parker dominance index; $S$ = number of species; $N$ = number of records; MC = Marula/Combretum sand savanna; GC = Grassland savanna clearings; MT = Mixed Tree savanna; CB = Calc brack thicket; RT = Riverine thicket. "TOTALS" refers to the overall diversity indices for each season and is based on all samples irrespective of habitat, location of pitfall traps or the time of day.

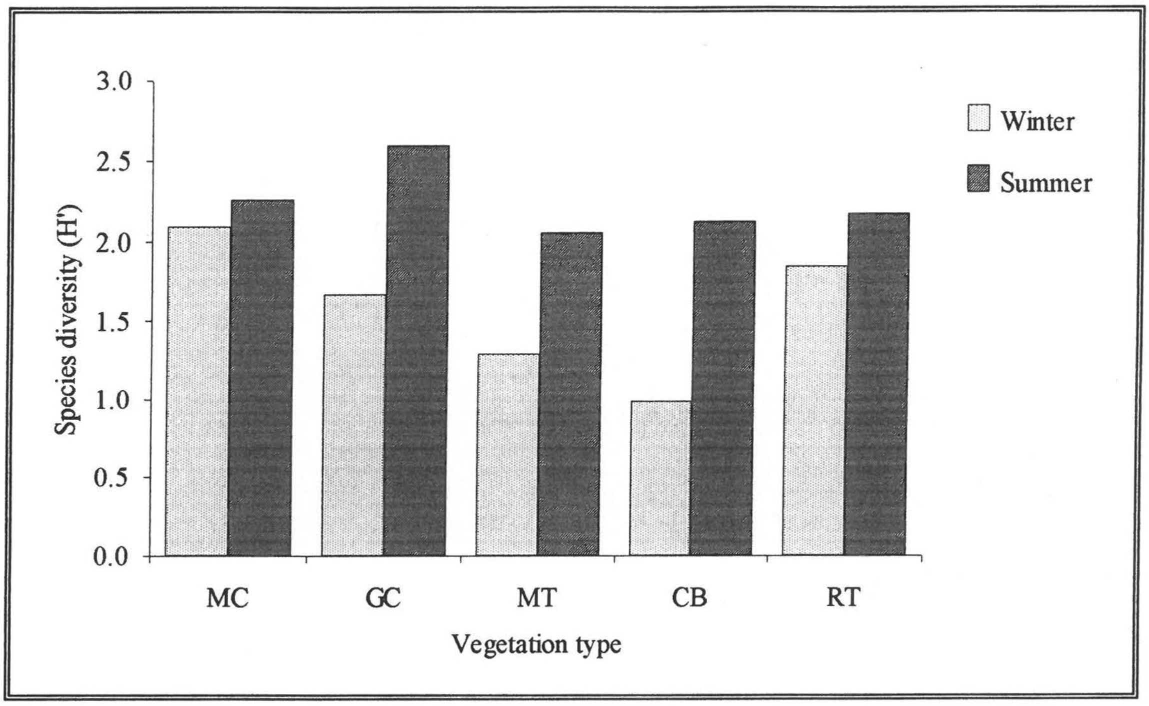


**Fig. 3.4.** The seasonal difference in the diversity index $(H')$ for ants and termites caught in pitfall traps in five different habitat types.

marula/*Combretum* site differed between summer and winter by only 7%, whereas in the other sites the difference was at least 15%. The greatest difference in diversity between summer and winter was 53%, and was recorded in the calc brack (CB) site (Table 3.3).

During summer the diversity and evenness of distribution of ants and termites located in exposed areas was higher than in shaded areas, whereas during winter the diversity and evenness of distribution was higher in shaded areas (Table 3.3). In addition, the diversity and evenness of distribution was higher during summer for both exposed and shaded areas.

The diversity and evenness of distribution of diurnal activity of ants and termites were higher than the nocturnal activity during summer and winter (Table 3.3). These indices were also higher during summer for both the diurnal and nocturnal activities.

The overall species richness *(S)* was highest in the marula/*Combretum* site where a total of 42 species was recorded, while the lowest species richness ($S = 30$) was recorded in the mixed tree site (Table 3.1). Thus the diversity index *(H')* did not appear to be influenced by species richness. Instead the higher diversity *(H')* indices were mainly due to the higher evenness of distribution *(J')* of species within the site (Table 3.3). Species richness was higher during summer than winter for all sites (Table 3.3; Fig. 3.5.).

The highest percentage of dominance *(d)* by a single species of 44.7% was recorded in the calc brack site during winter, and the lowest (24%) was also recorded in the calc brack site but during summer (Table 3.3). The single species dominance in the various sites was due to three ant species, namely:

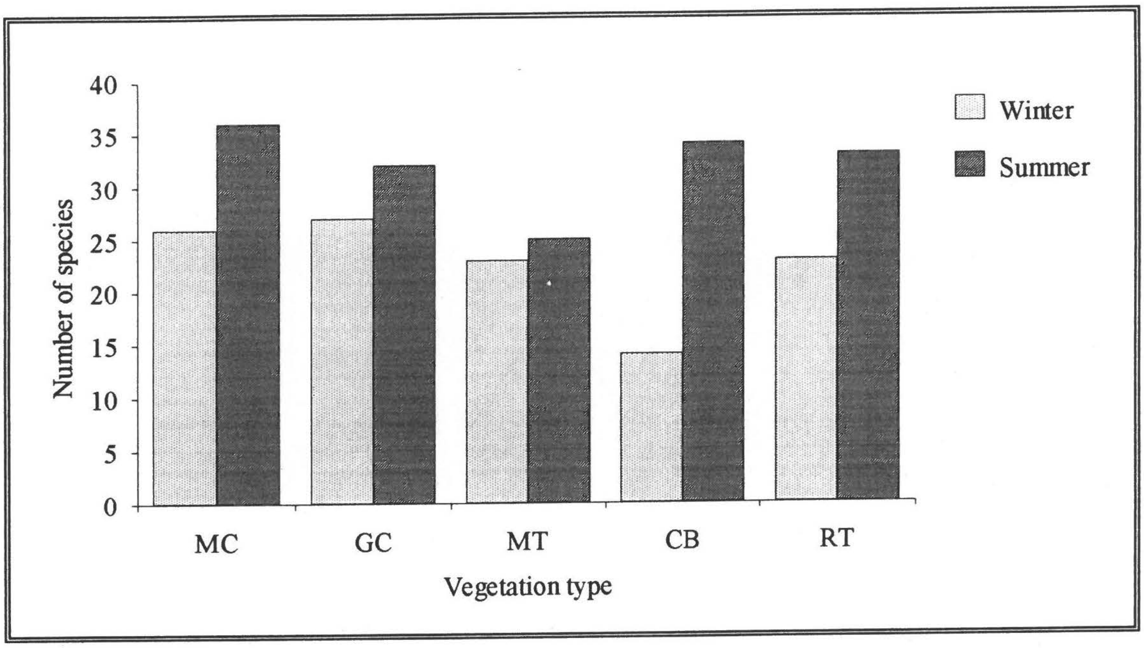


**Fig 3.5.** Seasonal differences in the total number of species caught in pitfall traps in five different habitat types.

*Pheidole* sp. 2; *M. damarense*; and *A. custodiens* (Berger-Parker dominance indices given in Table 3.3). *Pheidole* sp. 2 was the most dominant species in the grassland and riverine sites during summer and winter, the mixed tree site during summer, and the marula/*Combretum* site during winter. *M. damarense* dominated the marula/*Combretum* site during summer, and the mixed tree and calc brack sites during winter. *A. custodiens* was dominant only in the calc brack site and only during summer.

## Activity

The frequency of occurrences in pitfall traps ($N_1$) of all species of epigaeic ants and termites is given in Table 3.1. Activity is given as $N_1$ divided by the appropriate number of pitfall checks. Thus, the overall activity for each site is equal to the total $N_1$ divided by 1296 (total number of pitfall checks per site). The highest overall activity of 1.047 was recorded in the grassland savanna site and the lowest value (0.688) was recorded in the calc brack site.

Of the 55 species of ants and termites recorded, only 10 (18%) were active every month and 14 (25%) were more active during winter. The overall activity was significantly higher during summer than during winter ($\chi^2 = 281.5$; df = 1; $p < 0.001$). Although the activity in individual sites also appeared higher during summer (Fig. 3.6), the difference between summer and winter was not significant for the riverine (RT) site ($\chi^2 = 2.6$; df = 1; $p > 0.1$). There was a significantly higher activity of ants and termites during summer in the marula/*Combretum* (MC) site ($\chi^2 = 7.5$; df = 1; $p < 0.007$), the grassland (GC) site ($\chi^2 = 143.6$; df = 1; $p < 0.001$), the mixed tree (MT) site ($\chi^2 = 74.7$; df = 1; $p < 0.001$), and the calc brack (CB) site ($\chi^2 = 159.8$; df = 1; $p < 0.001$).

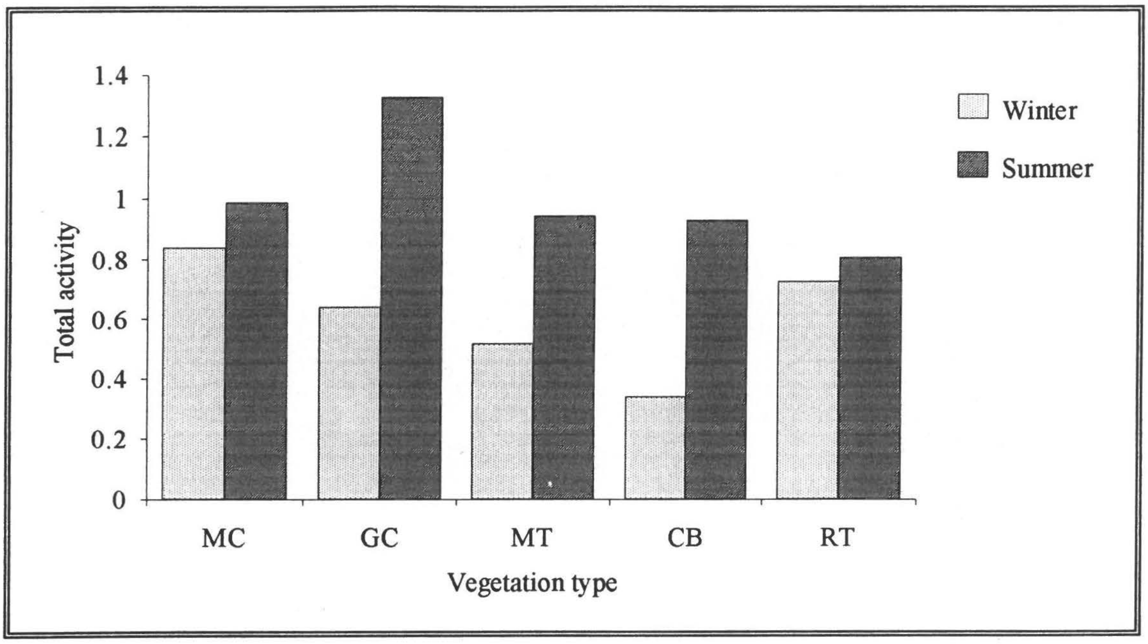


**Fig. 3.6.** The seasonal activity of all epigaeic ants and termites collected in pitfall traps. Total activity = $\Sigma p_i$ where $p_i$ = the proportion of pitfall samples where species *i* was found.

The pugnacious ant *A. custodiens* was the predominant prey species in the pangolins' diet (see chapter four), therefore it is worthwhile comparing this species activity within the various sample sites (Fig. 3.7). Only 8.1% of the overall activity of this species was recorded during winter, whereas the balance of 91.9% was recorded in summer. In addition, 62.4% of the total activity of this species was recorded in the calc brack (CB) site during summer and only 4.4% during winter (Fig. 3.7).

The overall activity of epigaeic ants and termites that were located in areas not shaded by shrubs or trees was significantly higher than those located in shaded areas (Mann-Whitney U test, $U = 117$; $n_1 = 13$; $p < 0.001$; the 99.9% confidence interval calculated for U is $52.6 \leq U \leq 116.4$). The proportion of activity in shaded and exposed locations are illustrated in Fig. 3.8. During the summer months, when temperatures were higher, the activity of ants and termites appeared higher in the exposed areas than in the shaded areas (Fig. 3.8). In contrast, the proportion of activity was higher in the shaded areas during June and July, the coldest months of winter (Fig. 3.8). The proportion of activity of ants and termites recorded in exposed areas each month correlated significantly with the mean monthly minimum temperatures between July 1993 and July 1994($r = 0.85$; $df = 11$; $p < 0.001$).

The diel activity of ants and termites deduced from pitfall trap catches is depicted in Fig. 3.9. Pitfall catches indicate that six (60%) of the most abundant species were predominantly diurnal while 40% were predominantly nocturnal. The overall diurnal activity of epigaeic ants and termites made up 58% of the total pitfall samples while the remaining 42% was due to nocturnal activity. The nocturnal activity proved significantly lower than the diurnal activity (Mann-Whitney U test, $U = 52$; $n_1 = 13$; $p < 0.001$; the 99.9% confidence interval

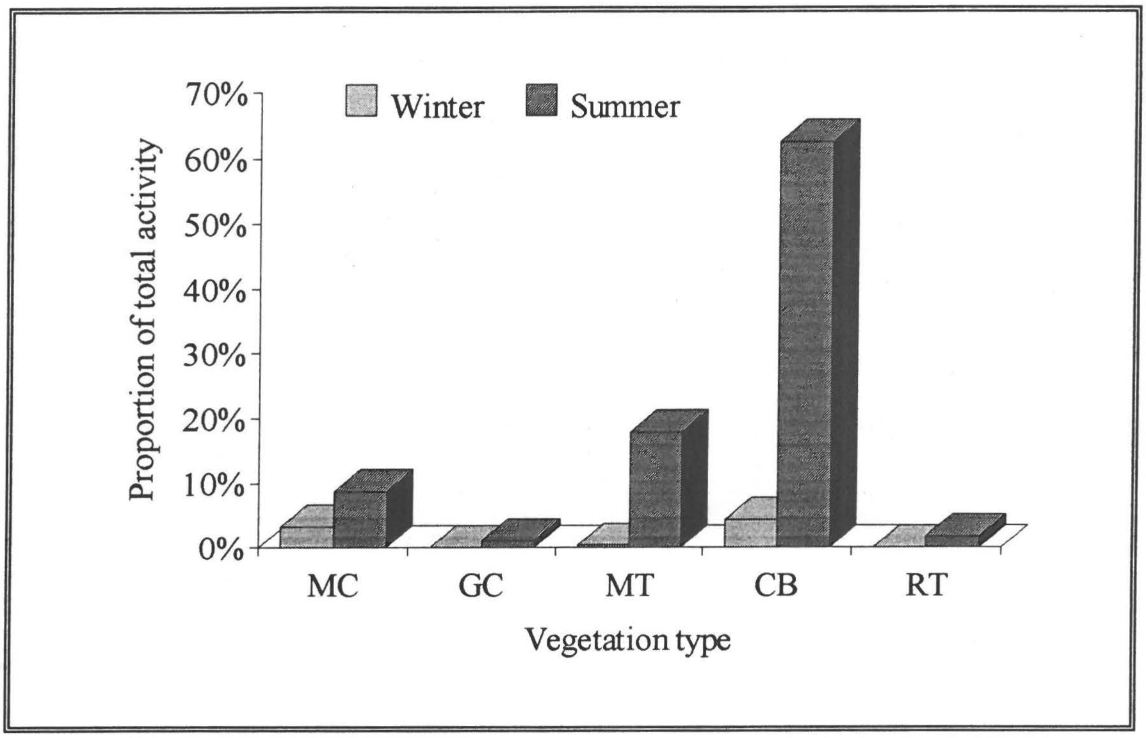


**Fig. 3.7**. The seasonal activity of *A. custodiens* sampled in pitfall traps and recorded as a percentage of the total activity of this species.

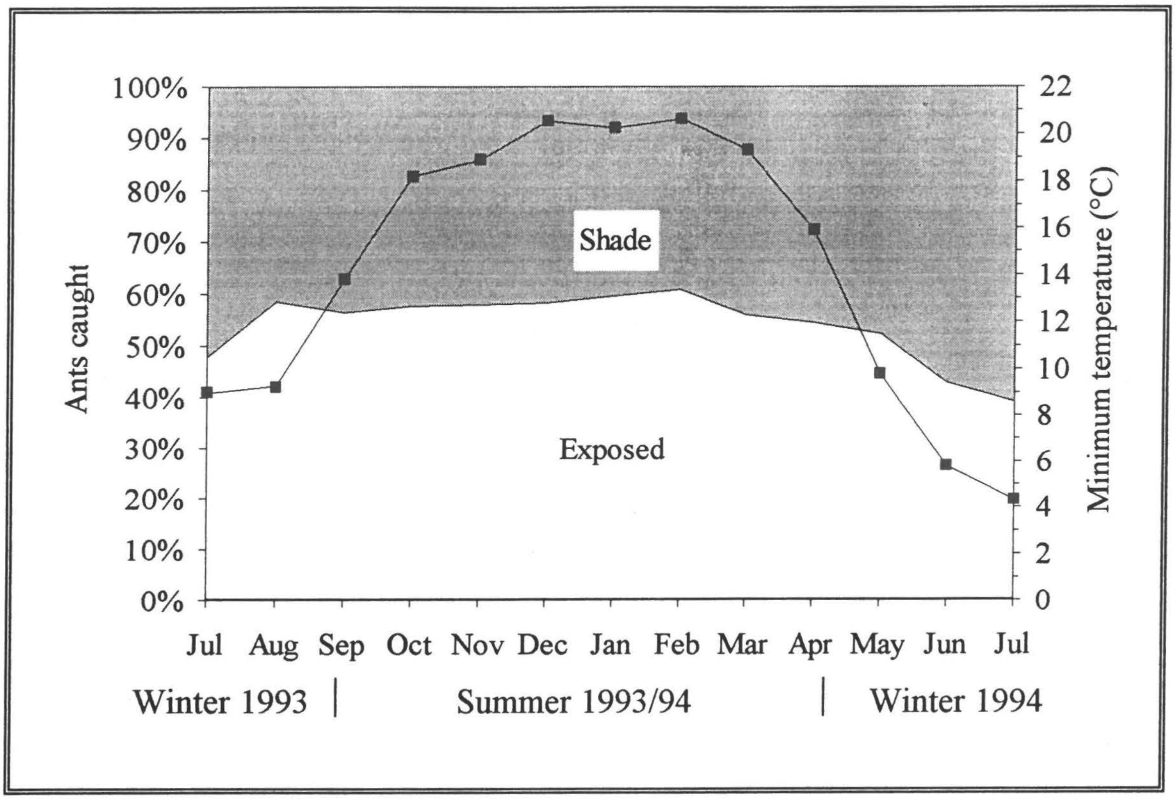


**Fig. 3.8.** The proportion of epigaeic ants and termites (percentage of total activity) that were active in locations shaded by a tree or shrub canopy and locations openly exposed. The minimum temperature (right axis) is included to show the relationship between temperature and location of activity.

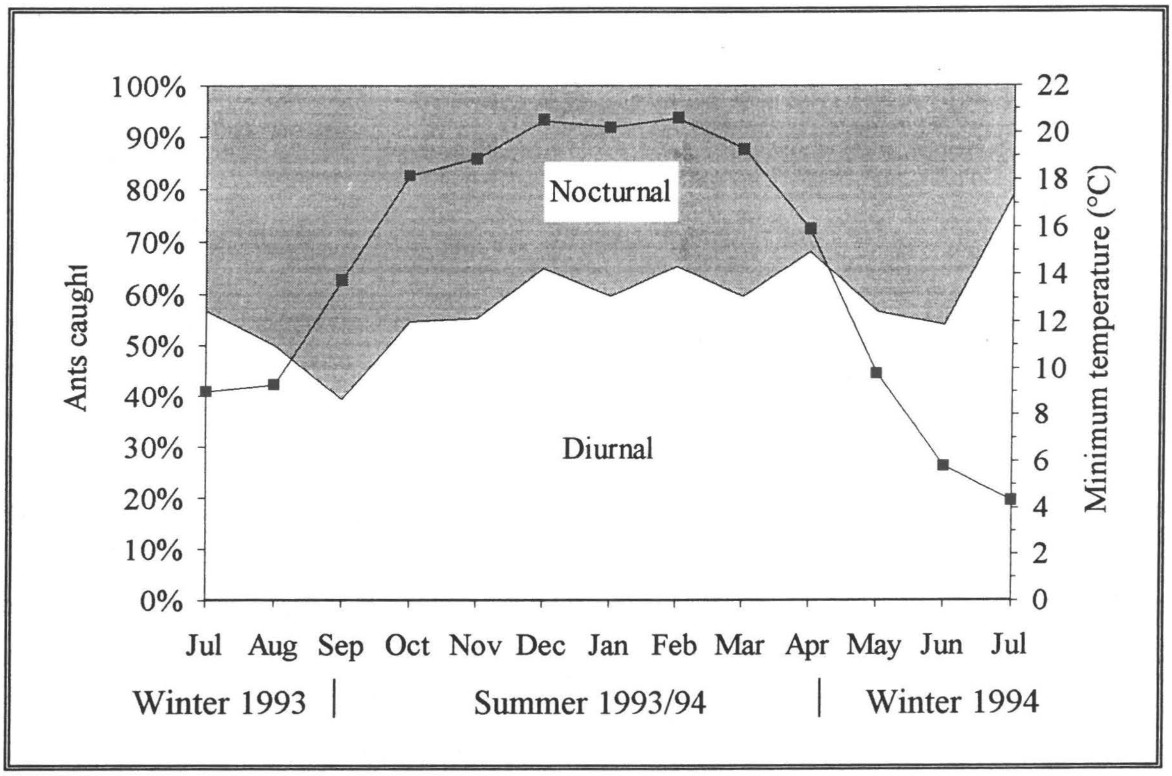


**Fig. 3.9.** The proportion of epigaeic ants and termites (percentage of total activity) that were diurnally and nocturnally active over a 13 month period. The mean minimum temperature (right axis) is included to show the relationship between temperature and diel activity.

calculated for U is $52.6 \leq U \leq 116.4$). Interestingly, the ant species *Pheidole* sp. 3 switched from a predominantly diurnal activity during winter, to a predominantly nocturnal activity during summer. Similarly, the termite species *Hodotermes mossambicus* switched from being mainly diurnal during summer to mainly nocturnal during winter.

The seasonal activity of the six most important species of ants and termites preyed on by pangolins are represented in Fig. 3.10 (refer to chapter 4 for the occurrence of these species in the pangolin's diet). The pugnacious *ant A. custodiens* constituted the largest proportion of the pangolin's diet. The percentage occurrence of *A. custodiens* in pitfall traps was considerably higher than the other five species, especially during the period February 1994 to May 1994 when the occurrence of *A. custodiens* was greater than 85% (Fig. 3.10).

The seasonal activity patterns of *A. custodiens* together with rainfall and ambient temperatures are given in Fig. 3.11 and Fig. 3.12. The overall activity of this species was very low during winter, gradually increasing in early summer with a sudden peak during February and then a steep decrease at the end of summer. Although there was no significant correlation between rainfall and the activity of *A. custodiens* ($r = 0.29$; $df = 11$; $p > 0.3$), there is a significant correlation between their activity and the minimum temperatures ($r = 0.56$; $df = 11$; $p < 0.05$). The activity of *A. custodiens* also appears to be higher in exposed areas compared to areas shaded by vegetation (Fig. 3.11). In addition, the diurnal activity of this species was also considerably higher than the nocturnal activity (Fig. 3.12).

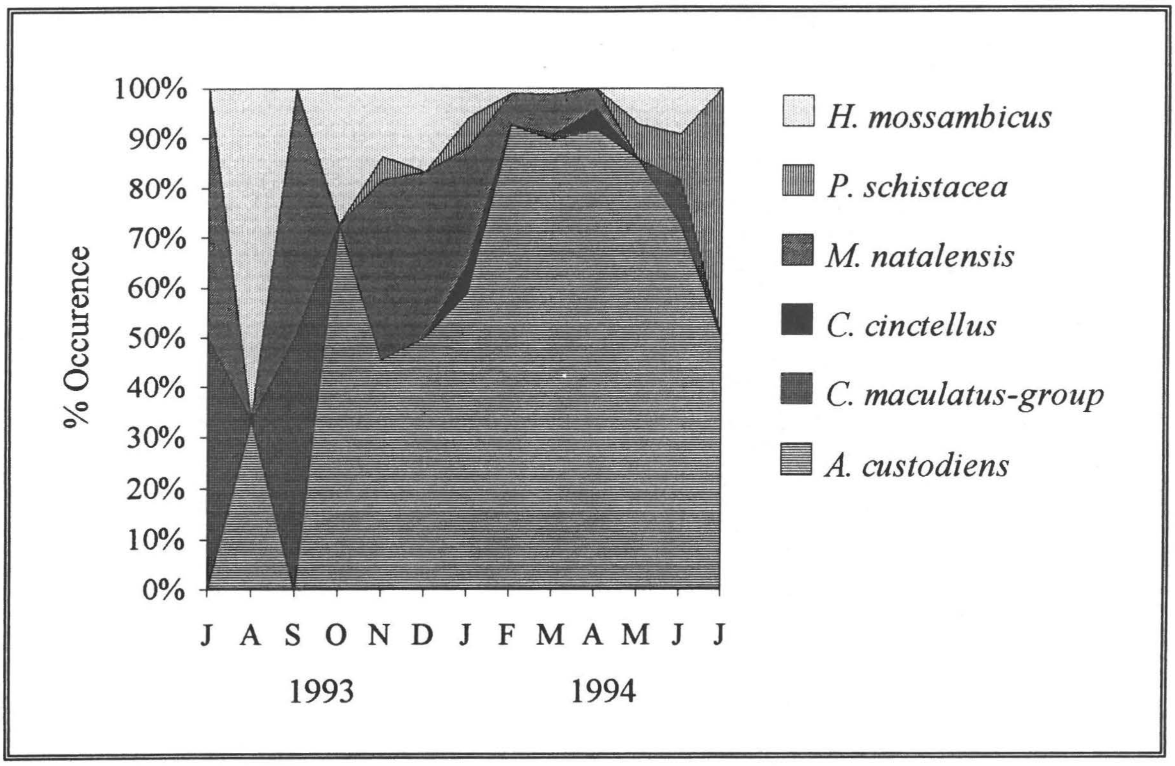


**Fig. 3.10.** Seasonal changes of occurrence in pitfall traps of the six most important prey species in the pangolin's diet. The percentage occurrence is given as the proportion of the total activity of these six species.

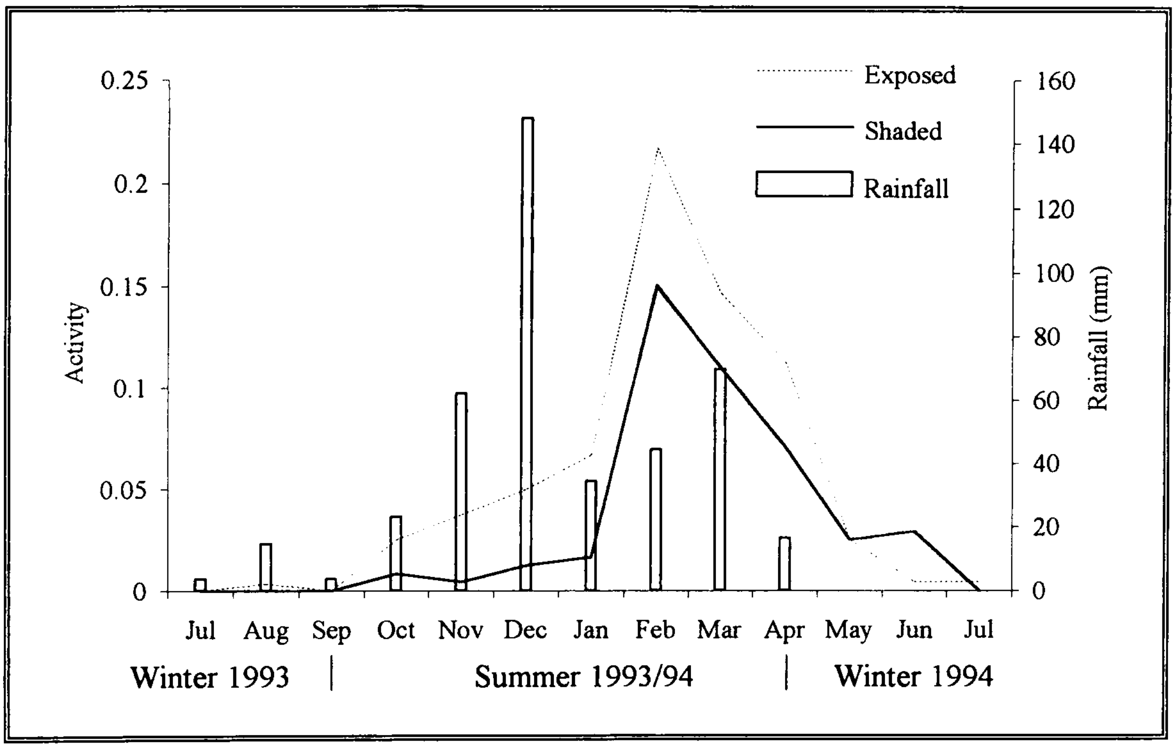


**Fig. 3.11.** Seasonal activity of *A. custodiens* sampled in pitfall traps situated in exposed and shaded areas. Activity = $p_i/\Sigma p_i$ where $p_i$ = the proportion of pitfall samples where species *i* was found.

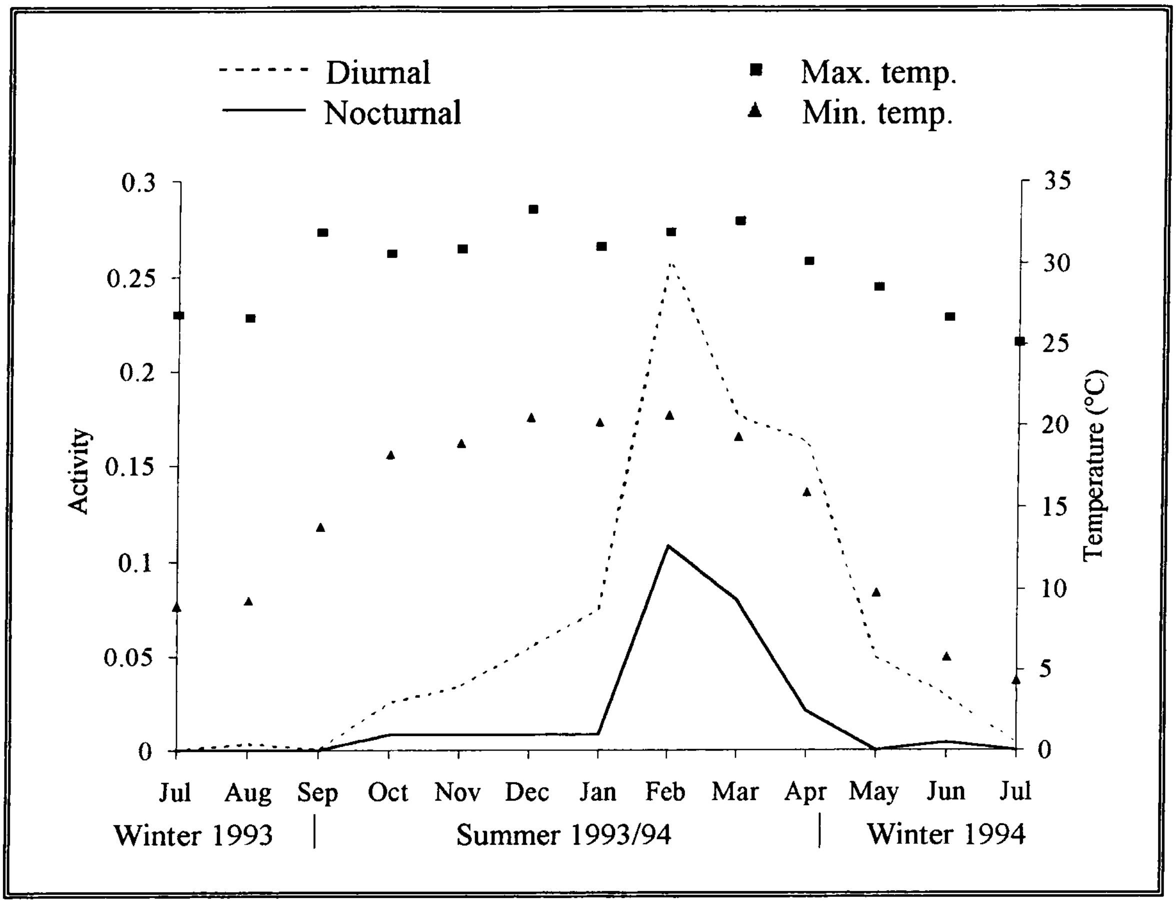


**Fig. 3.12.** The seasonal diel activity of *A. custodiens* sampled in pitfall traps over a 13 month period. Activity = $p_i/\Sigma p_i$ where $p_i$ = the proportion of pitfall samples where species i was found.

## DISCUSSION

### Assessment of pitfall sampling

Pitfall trapping is a popular method used to sample the activity of surface dwelling arthropods, and, although it is not effective for certain taxa (Briggs 1961; Hayes 1970), it is considered effective for sampling ant populations (Greenslade & Greenslade 1971; Greenslade 1973). The efficacy of this method in the present study was satisfactory, however, the abundance of certain species was over estimated and other species were under estimated. This may be attributed to at least two factors.

Firstly, the different behaviour of species makes them differentially susceptible to capture in pitfall traps. For example the fast moving *A. custodiens* was frequently observed to dash across the soil surface straight into a pitfall trap, resulting in a large number of individuals occurring in a single sample (Table 3.1). On the other hand, slow moving species such as *P. schistacea* and *M. natalensis* were often observed skirting the perimeter of the pitfall trap before heading off in another direction. In addition, these two species and the *Camponotus* spp., although nesting underground, spent most of their time foraging in shrubs or trees without coming in contact with the traps, and were consequently under sampled (Table 3.1). The termite species were also under sampled and their low variety and abundance represented in Table 3.1 is largely a result of most species being subterranean.

Secondly, the dense aggregations of ants arising from their colonial habits may also induce biased results. On several occasions the placement of pitfall traps in close proximity to active nests appears to have resulted in a distortion of the data. For example, 2850 individuals of *A. custodiens* were collected in one pitfall trap in 23 records. Thus, 35% of all recordings of this species are from one pitfall, and probably represent the activity of a single colony. Other species such as *Pheidole* sp. 2, *H. mossambicus* and *M. junodi* were also affected by this distortion, although not as seriously as *A. custodiens*.

## Composition of the ant and termite fauna

Each habitat type or sample site has a pronounced difference in vegetation and soil that is matched by a marked difference in the species composition of ants and termites. This is consistent with the widespread finding that distinctive ant assemblages are often associated with different vegetation types (Brian 1964; Brown 1959; Cole 1934; Greenslade & Greenslade 1977; Hayashida 1960; Majer 1972; Weber 1943). Plants provide ants with important food sources and nesting sites, and they act as hosts to honeydew-producing mutualists that supply the ants with honeydew. In addition, fauna associated with the vegetation may interact as potential prey, predators and competitors of ants (Bequaert 1922; Buckley 1982; Skaife 1979).

The structural differences of the various soil forms probably also play an important role in the distribution of the subterranean nests of certain ant and termite species. For example, the density of *A. custodiens* nests appear higher in areas of more compacted clay soils (pers. obs.). Steyn (1954) noted that the nest entrances situated on a sandy soil surface would often cave in if a large *A. custodiens* replete (ant swollen with honeydew) attempted to pass through it.

It is generally accepted that there is often an association between soils and vegetation (Anderson & Talbot 1965; Dye & Walker 1980; Lathwell & Grove 1986; Morrison, Hoyle & Hope-Simpson 1948; Russel 1973; Venter 1986), and thus the preference of ants for a particular area is probably determined by a combination of vegetation and soil type. This was evident, particularly with *A. custodiens* in the calc brack (CB) site, where this species was often seen in large numbers on the shrub *Euclea divinorum* where they were tending homopterans for honeydew. In contrast, in other areas where this shrub also occurred frequently, *A. custodiens* and its symbionts were absent (pers. obs.).

## Species diversity

As is the case in this study, semi-arid regions are often rich in ant species, since ants are physiologically and behaviourally adapted to extreme temperatures and encounter little competition from other arthropods (Greenslade 1979).

According to Greenslade (1979) the ideal habitat for ants is a mosaic of bare soil and areas of forbs, small shrubs and grasses under an open canopy of trees or taller shrubs. The bare soil is ideal for nest excavation and allows unhindered foraging, while food is provided by the flora in the form of exudates, insect prey, seeds and honeydew-producing insects. The litter from trees and tall shrubs provides shelter for cryptic ants and helps buffer against extreme surface temperatures and moisture loss. The vegetation structure of the grassland savanna clearings (GC) is similar to this "ideal" habitat and probably accounts for the higher overall diversity in this area.

Previous investigations on birds (MacArthur & MacArthur 1961), desert lizards (Pianka 1967) and homopterans (Murdoch, Evans & Peterson 1972) have indicated a direct correlation between structure of vegetation and diversity in these groups. Room (1975) noted that heterogeneity of habitat could account for variability in the species richness of a tropical ant fauna, although human interference, stage of succession, and interspecific interactions between ants were important factors that modified the intrinsic diversity. In the present study, however, diversity in the grassland savanna (GC) site did not appear to be reduced by the loss of the shrub layer by mechanical clearing. Instead, the diversity may have increased since patches of bare soil remained after the clearing operation and many of the shrubs were replaced by forbs and grasses, resulting in a vegetation structure similar to Greenslade's "ideal" habitat for ants.

In arid and semi-arid regions where temperatures are often extreme, ant activity is apparently controlled by changes in temperature and food supply, and regulated by daily weather fluctuations (Whitford 1978; Briese & Macauley 1980; Majer 1980; Andersen 1983, 1986; Greenslade & greenslade 1984). This study was no exception since the abundance and diversity of ants was considerably higher in summer than in winter, which is in accordance with the results of other regions in South Africa (see Koen & Brytenbach 1988 and Willis, Skinner & Robertson 1992).

Temporal differences in diversity between sites were somewhat surprising since the different sites were no more than three kilometres apart. However, cold air drainage into the valley bottoms during winter, which results in lower minimum temperatures in the valley bottoms than the upper slopes and crests (Barbour, Burk & Pitts 1987), may account for the differences. This phenomenon could explain why the ant diversity of the marula/Combretum (MC) site, situated on the crest of the hill, was affected less by the difference in summer and winter minimum temperatures than the other sites (Table 3.3). In addition, the higher ant diversity and activity of the marula/*Combretum* site during winter (Table 3.3; Fig. 3.6) is probably also as a result of the difference in temperature between the crests and the valley bottoms.

## Activity

The pronounced seasonality in the patterns of foraging activity exhibited by the ant communities described here, is characteristic of ant communities, particularly those of regions that experience extreme seasonal fluctuations in temperature and food availability (Cole 1934; Whitford 1978; Briese & Macauley 1980; Andersen

1983). During winter there was a general reduction in activity and as conditions became warmer activity increased. These conditions resulted in a marked separation of species in time, since only 10 of the 55 species were active all year round, and 25% of all species were more active during winter. This probably represents a form of time partitioning (Schoener 1974), due to long term interspecific competition, which appears to play an important role in species coexistence (Briese & Macauley 1980; Andersen 1983).

Temperature, as a major factor influencing ant activity, has frequently been noted in the past (Cole 1934; Steyn 1954; Holt 1970; Sanders 1972; Briese & Macauley 1980; Andersen 1983), and appears to be the major factor controlling ant activity during this study. However, micro-climate modifications by plants and their litter may also influence ant activity (Brian & Brian 1951; Yeatman & Greenslade 1980). This is evident by the significant increase in the proportion of ant activity in the shade as temperature decreased, especially during the winter months of June and July (Fig. 3.8). Moreover, the minimum temperature of July 1994 was considerably lower than July 1993, which probably resulted in a higher proportion of activity in the shade during July 1994 compared to July 1993 (Fig. 3.8). The litter from the trees and shrubs provides shelter and probably acts as a buffer against the extreme cold during the coldest months.

The diel activity of ants also appears to be influenced by cold conditions. In a study of an ant community in a semi-arid region of Australia, Briese & Macauley (1980) reported that many species switched from nocturnal to diurnal foraging when conditions became colder. This pattern appears to be a common feature of ant communities, particularly in arid regions where extreme fluctuations in temperature and food availability are prevalent (Cole 1934; Whitford 1978). Although the overall diurnal activity did not appear to be determined by temperature, the diurnal activity during July 1994 was considerably higher than the other months, including July 1993. This was probably as a result of the much colder conditions experienced during July 1994. Thus, for each species of ant, there may be a threshold minimum temperature below which they become inactive until the daytime when conditions become warmer, and their activity becomes predominantly diurnal.

The activity of one species, the pugnacious ant *A. custodiens,* appeared to decrease considerably with cold temperatures (Fig. 3.12), so much so that their activity during winter was 11 times lower than during summer. This was probably because most of the major and median workers hibernated during winter while the rest of the workers, mainly minor workers, continued to forage throughout winter (Steyn 1954).

The sudden rise in activity of *A. custodiens* during February 1994 can probably be ascribed to the high rainfall recorded during December 1993 (Fig. 3.11). This is similar to the pattern of activity of *A. custodiens* reported in Bloemfontein (cf. Louw 1968), where high rainfall was recorded during January 1966, followed by a sudden increase in activity during March 1966. The two month delay is possibly related to the life cycle of the homopterans that supply the ants with honeydew. According to Steyn (1954) approximately 99% of the diet of *A. custodiens* consists of honeydew, thus a sudden increase in the numbers of these honeydew producing mutualists would more than likely result in a similar increase in the activity of *A. custodiens.*

Since the study area is rich in ant species and several species are abundant, there appears to be a readily available supply of prey for pangolins. However, the activity and size of the various species, and the pangolin's ability to locate and dig open the underground nests and galleries may be as important in determining their viability as prey. Pangolins are nocturnal forages thus it is important that their prey is available at night. This means that their ant prey should be relatively inactive at night and close to the soil surface. In general, the nocturnal activity and diversity of ants was lower than the diurnal activity and diversity. The pangolin's preferred prey species *A. custodiens* was considerably less active at night. In addition, *A. custodiens* was much more active during summer than winter and was therefore expected to be preyed on less often during summer months. In contrast, the termite species most commonly preyed on by pangolins *H. mossambicus* was only preyed on when they were active (see Chapter 4). This species switched from being predominantly diurnal during summer to predominantly nocturnal during winter, thus making them more available to pangolins during winter.

There was a considerable variation in the composition of ants and termites in the various habitats. Where the calc brack habitat is included within a pangolin's home range, this habitat should be selected in preference to other habitats as foraging areas since *A. custodiens* was four times more common in this habitat type. However, since the activity of *A. custodiens* was 11 times greater during summer in the calc brack areas, pangolins were also predicted to forage less in this habitat during summer.

Besides establishing the diel and seasonal composition, diversity and activity of ants and termites, and their availability as prey to pangolins, several predictions were made on the pangolins feeding behaviour. These will be discussed in the following two chapters.

# CHAPTER 4

# ACTIVITY, DIET AND FORAGING BEHAVIOUR OF PANGOLINS

## INTRODUCTION

Although there have been no detailed studies on the activity of *M. temminckii* before the present study, they are recorded as being nocturnal and partially diurnal animals (Dorst & Dandelot 1970; Kingdon 1971; Smithers 1983). This chapter describes the daily and seasonal activity patterns of *M. temminckii* in detail to establish whether temperature and prey activity influence the activity of pangolins. The difference between the activity of adult and sub-adult pangolins is also examined, and their preferred temperature range of activity is determined.

According to Smithers (1983) *M. temminckii* prey predominantly on formicid ants, which include the species *Camponotus thales*, *Anoplolepis custodiens* and *Paltothyreus tarsatus*. In East Africa, Kingdon (1971) rated them as selective feeders of ants and termites, feeding primarily on the juvenile stages of *Crematogaster*, *Odontotermes* and *Microcerotermes*. Jacobsen *et al.* (1991) recorded 13 species of ants from the family Formicidae and three species of termites in the diet of *M. temminckii*. Since the diet of pangolins appears to vary between different geographical locations, the aim of the present study was to establish: (a) the composition of their diet in the present study area; and (b) the relative importance of the various prey species in relation to their availability.

The daily and seasonal variation in foraging behaviour of pangolins is also examined. The methods used by pangolins to locate prey and the various feeding strategies they adopted in response to the predator defence of their prey are discussed in detail.

## METHODS

### Activity

Since pangolins are predominantly nocturnal and usually only emerge from their dens in the evening, it was essential to locate their dens during the day so that the time they became active could be monitored. Once a pangolin's den was located, one of two methods was used to determine the time that it left and returned to the den.

One method was to wait a distance of approximately 100 metres from the den until the pangolin emerged. The amplitude of the radio signal received from the pangolin's radio transmitter was relatively low while underground. Thus, an increase in the signal amplitude indicated that it had emerged from the den. The time and ambient temperature were then recorded and the animal was followed on foot until it returned to a den, when the time and temperature were recorded again. Temperatures were recorded to determine whether there was any correlation between ambient temperature and the pangolin's activity.

An alternative method used was by means of a "home made" digital recorder installed at the pangolin's den. The recorder was linked to a radio receiver tuned to the pangolin's transmitter and placed in a waterproof container. The signals received from the pangolin's radio transmitter were recorded and stored by this digital recorder. The sensitivity of the recorder was adjusted so that the signals were only received by the recorder while the pangolin was in the den. Thus, the date and time could be calculated when the pangolin exited or entered the den. This system was particularly useful since more than one pangolin's activity could be monitored simultaneously.

## Foraging behaviour and diet

To determine where the pangolins were foraging, and whether they foraged in the same area on consecutive evenings, it was necessary to establish the location of each feeding and the distances between feedings. The distance between each feeding bout was paced out or estimated in 10 m intervals and recorded, while the longitude and latitude co-ordinate of the pangolin's position was stored in the memory of a Global Positioning System (GPS) at 50 m intervals. This distance seemed reasonable since the GPS usually operated within an accuracy of between 20 and 35 m. The GPS continually displayed the expected positional error (EPE) and co-ordinates were only stored when the EPE was less than 35 m.

The digging duration required to expose each prey species, and duration of each feeding bout was timed with a stop watch. The duration of each feeding bout on each ant or termite species was timed after the foraging tunnel or nest was opened, so that the duration did not include digging time. Digging was clearly observed on most occasions since the body is jerked when the front claws are digging, while it remains absolutely still when the pangolin is feeding (pers. obs.).

The depth of all holes excavated by pangolins to expose the foraging tunnels or nests of each species of ant and termite was measured with a tape measure and recorded as dig depth. The feeding digs were classified as follows: "P" was recorded when a pangolin fed directly from an open ant or termite port; "L" when termite nests in logs, branches or twigs were scratched open; "S" when ants or termites were preyed on from the surface of the soil; and "G" when ants and termites were preyed on from excavations in the soil. Ant and termite species exposed by the pangolins during feeding were collected, sorted and preserved in alcohol. All ant species were identified by Dr. H.G. Robertson, and housed in the

South African Museum collection, Cape Town, while termite species were identified by Mrs V.M. Uys (National Collection of Insects, Pretoria).

## RESULTS

A total of 18 pangolins was located in the study area and they are listed in Table 4.1. These included four adult males, eight adult females, four sub-adult females, one sub-adult male and one sub-adult of unknown sex. The number of hours of data depicted in Table 4.1 refers to feeding data only and since five of these pangolins were very disturbed when being followed, no data was collected on their feeding behaviour. Fifteen of the 18 pangolins were tagged with radio transmitters and the weight of each animal is listed in Table 4.1. The average weight of adult males is 13.7 kg ( range = 12.6 kg - 16.1 kg; n = 4) and females 12.2 kg (range = 10.2 kg - 14.1 kg; n = 8). Although adult males are slightly heavier than adult females the difference is not significant (Mann-Whitney U test; $U = 24$, $n_1 = 4$, $P > 0.1$).

The activity of 18 pangolins (11 adults and seven sub-adults) and the feeding behaviour of 11 pangolins (10 adults and one sub-adult) was recorded over a period of 14 months (June '93 - July '94).

### Activity

Pangolins in the Sabie Sand Wildtuin (SSW) were usually inactive during the day and spent these hours resting in disused aardvark *Orycteropus afer* or warthog *Phacochoerus aethiopicus* dens (pers. obs.). Their activity was usually unpredictable since they may emerge from their dens any time between 15h00 in the afternoon and 02h15 the following morning. The activity period of 17 pangolins is summarised in Table 4.2.

**Table 4.1.** Data accumulated from pangolins during the study period (June '93 - July '94). All animals were tagged with radio transmitters except the sub-adults SA1, SA2 and SA3.

| Animal | Weight (kg) | Date caught | No. of days observed | No. of hours of data |
|---|---|---|---|---|
| **Adult males** | | | | |
| Jobu | 12.6 | 07/04/93 | 74 | 68.7 |
| Zinga | 13.0 | 07/04/93 | 31 | 5.1 |
| Shumi | 13.2 | 19/09/93 | 41 | 60.1 |
| Zimu | 16.1 | 24/07/94 | 2 | 0.4 |
| **Adult females** | | | | |
| Nina | 14.1 | 05/04/93 | 50 | 52.9 |
| Thamo | 11.8 | 18/06/93 | 11 | 0.3 |
| Yela | 12.7 | 15/07/93 | 21 | 26.4 |
| Ozela | 14.0 | 28/07/93 | 38 | 48.4 |
| Vunga | 10.8 | 05/09/93 | 41 | 33.3 |
| Lola | 12.6 | 11/11/93 | 11 | 1.9 |
| Penula | 10.2 | 13/03/94 | 12 | 2.1 |
| Azana | 11.4 | 02/06/94 | 6 | 1.5 |
| **Sub-adults** | | | | |
| Nyane | 4.7 | 04/04/93 | 4 | 0 |
| Imini | 6.2 | 11/06/93 | 26 | 30.5 |
| Kunja | 7.2 | 26/12/93 | 7 | 0 |
| SA1 | 4.9 | 09/02/94 | 2 | 0 |
| SA2 | - | 11/02/94 | 1 | 0 |
| SA3 | 5.5 | 14/02/94 | 1 | 0 |

**Table 4.2.** The time of day and temperatures when 11 adult and seven sub-adult pangolins were recorded exiting and entering their dens. Data on "Time active" excludes incomplete nights when pangolins were not observed exiting and entering a den. Standard deviations are enclosed in parentheses.

| | Mean time | Range | n | Mean temp. (°C) | Range (°C) | n |
|---|---|---|---|---|---|---|
| **Adults** | | | | | | |
| Leave den | 20h25 (02h07) | 14h34 - 02h15 | 163 | 18.1 (4.8) | 9 - 30 | 74 |
| Return to den | 00h20 (01h51) | 20h35 - 06h19 | 112 | 16.9 (5.0) | 7 - 25 | 101 |
| Time active | 03h51 (01h53) | 00h35 - 08h20 | 59 | 17.7 (4.5) | 4 - 30 | 194 |
| **Sub-adults** | | | | | | |
| Leave den | 18h02 (01h15) | 14h30 - 20h15 | 36 | 19.1 (4.1) | 10 - 25 | 16 |
| Return to den | 22h32 (02h12) | 19h42 - 01h32 | 7 | 13.8 (3.2) | 8 - 17 | 7 |
| Time active | 03h42 (01h26) | 02h27 - 05h17 | 3 | 16.4 (3.7) | 8 - 25 | 59 |

A total of 199 observations of pangolins leaving their dens and 119 of pangolins returning to their dens was recorded from June 1993 to July 1994. The majority of records (61%) of adult pangolins leaving their dens were between 19h00 and 22h00. Sub-adults on the other hand appeared to leave their dens earlier since 74% of these records were before 19h00 and the remaining 26% were between 19h00 and 01h00 ($n = 36$). Pangolins were usually only active for a relatively short duration each evening (see Table 4.2) and 47% of records of adult pangolins returning to their dens were before midnight. Most adults (83% of records) returned to their dens between 22h00 and 03h00. Sub-adults appeared to return to their dens considerably earlier than adults. Thus the sub-adult's pattern of activity was similar to adults except that it was approximately two hours earlier in all respects.

The seasonal variation and the comparison between the times that adult and sub-adult pangolins exited their dens are illustrated in Fig. 4.1. Sub-adult pangolins were recorded leaving their dens significantly earlier than adults during the winter months (Chi-squared test for sub-adults vs. adults; $\chi^2 = 16.91$, df = 8, $P < 0.04$). The same trend was observed during summer and the difference was highly significant (Fig. 4.1; $\chi^2 = 62.9$, df = 9, $P < 0.001$). In addition, adult pangolins left their dens significantly earlier during winter compared to summer ($\chi^2 = 48.83$, df = 10, $P < 0.001$). There was no significant difference between the times that sub-adult pangolins exited their dens during summer compared to winter ($\chi^2 = 5.82$, df = 4, $P > 0.2$). There was also no significant difference between summer and winter regarding the times that adult pangolins returned to their dens (Fig. 4.2; $\chi^2 = 11.94$, df = 9, $P > 0.2$). The difference between summer and winter could not be calculated since sub-adult pangolins were observed returning to a den during summer.

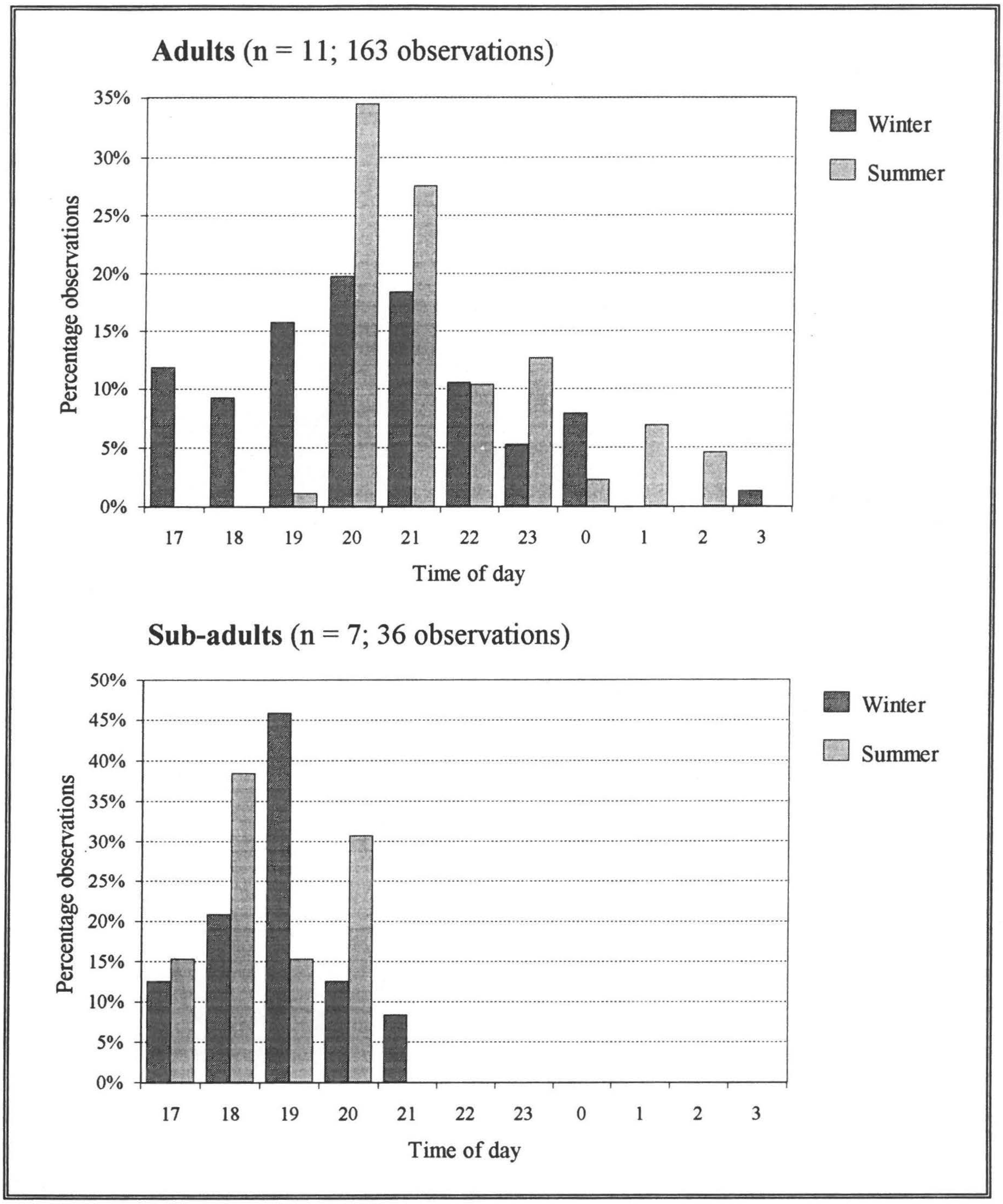


**Fig. 4.1.** The seasonal variation in the times that adult and sub-adult pangolins were observed leaving their dens. For the time of day; 17 = before 17h00, 18 = 17h00 to 17h59, 19 = 18h00 to 18h59, etc.

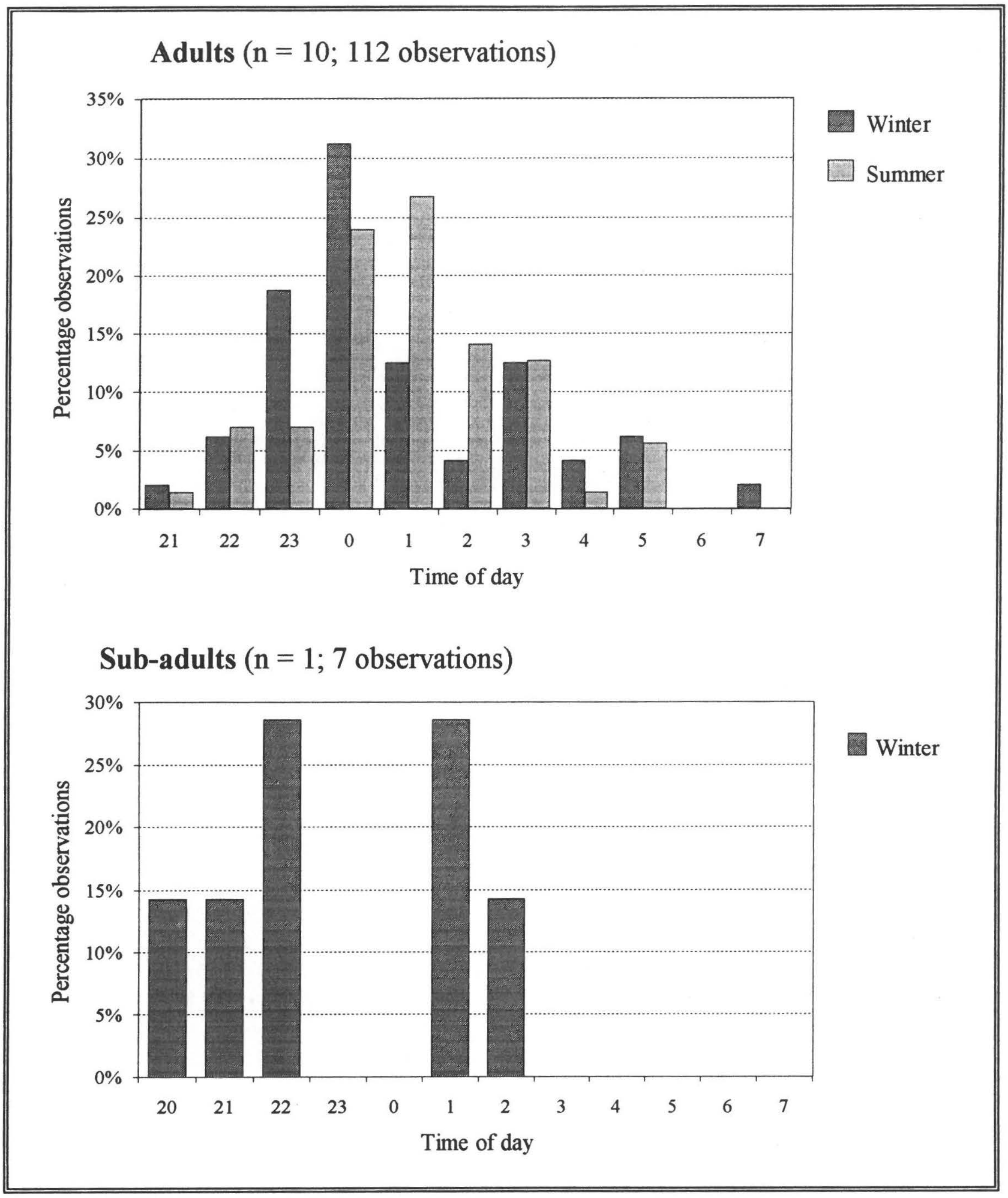


**Fig. 4.2.** The seasonal variation in the times that adult and sub-adult pangolins were observed returning to their dens. For the time of day; 20 = 19h00 to 19h59, 21 = 20h00 to 20h59, etc. No records of sub-adult pangolins returning to a den during summer were available.

The seasonal variation in the activity period of pangolins between June 1993 and July 1994 is illustrated in Fig. 4.3. The mean activity period of pangolins did not differ significantly between winter and summer (Mann-Whitney U test; U = 32.0, $n_1 = 6$, $P > 0.1$). Their activity period also appeared to remain constant throughout the year regardless of the time that they became active since there was a significant positive correlation between the time they left their dens and the time they returned (r = 0.62, df = 12, $P < 0.02$).

The time that pangolins remained active each evening appeared to be directly related to their feeding intensity (feeding time per hour). A recurrent pattern of high and low values of feeding intensity and activity time is evident in Fig. 4.4. During the months when their feeding intensity was lower they were active for longer during the evenings and *vice versa*. Thus, the mean feeding intensity recorded each month correlated significantly with the mean number of hours that pangolins were active (Spearmans rank correlation coefficient; $r_S = -0.7$, n = 14, $P < 0.01$). Although the feeding intensity varied considerably from month to month, there was no significant difference in feeding intensity between summer and winter ($t = 0.18$, df = 12, $P > 0.8$).

Pangolins were active throughout the year and were observed foraging in temperatures ranging from 4°C to 30°C, however their preferred temperature range of activity was from 11°C to 25°C (shaded regions of Fig. 4.5). There appears to be a difference between the preferred temperature ranges for adults and sub-adults. However, data on the activity of sub-adult pangolins was only accumulated during winter. The preferred temperature range of adults during winter was 11°C to 20°C which is similar to that of sub-adults. Thus, the overall preferred temperature range of sub-adults is probably similar to that of adults.

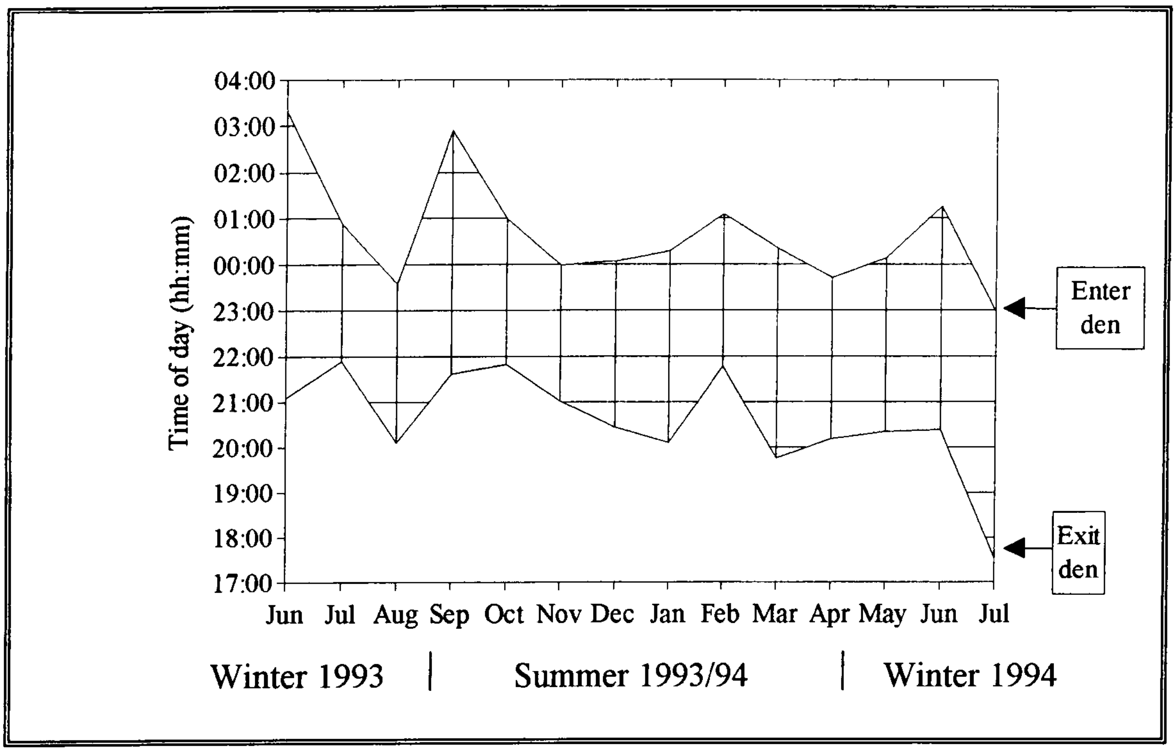


**Fig. 4.3.** The seasonal variation in the activity of adult pangolins depicting their mean activity period and the mean time that they exited and entered dens.

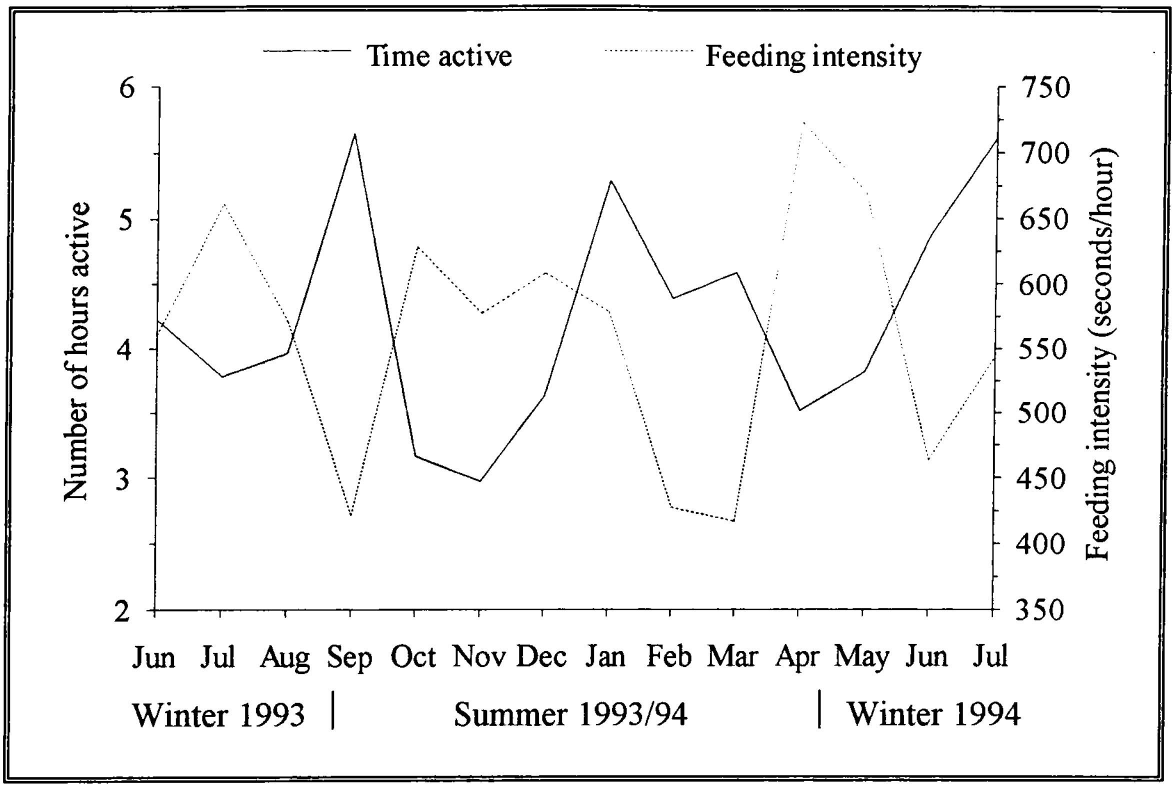


**Fig. 4.4.** The seasonal variation of the mean activity period recorded each month in relation to the mean feeding intensity ($r_S = -0.7$, $n = 14$, $P < 0.01$).

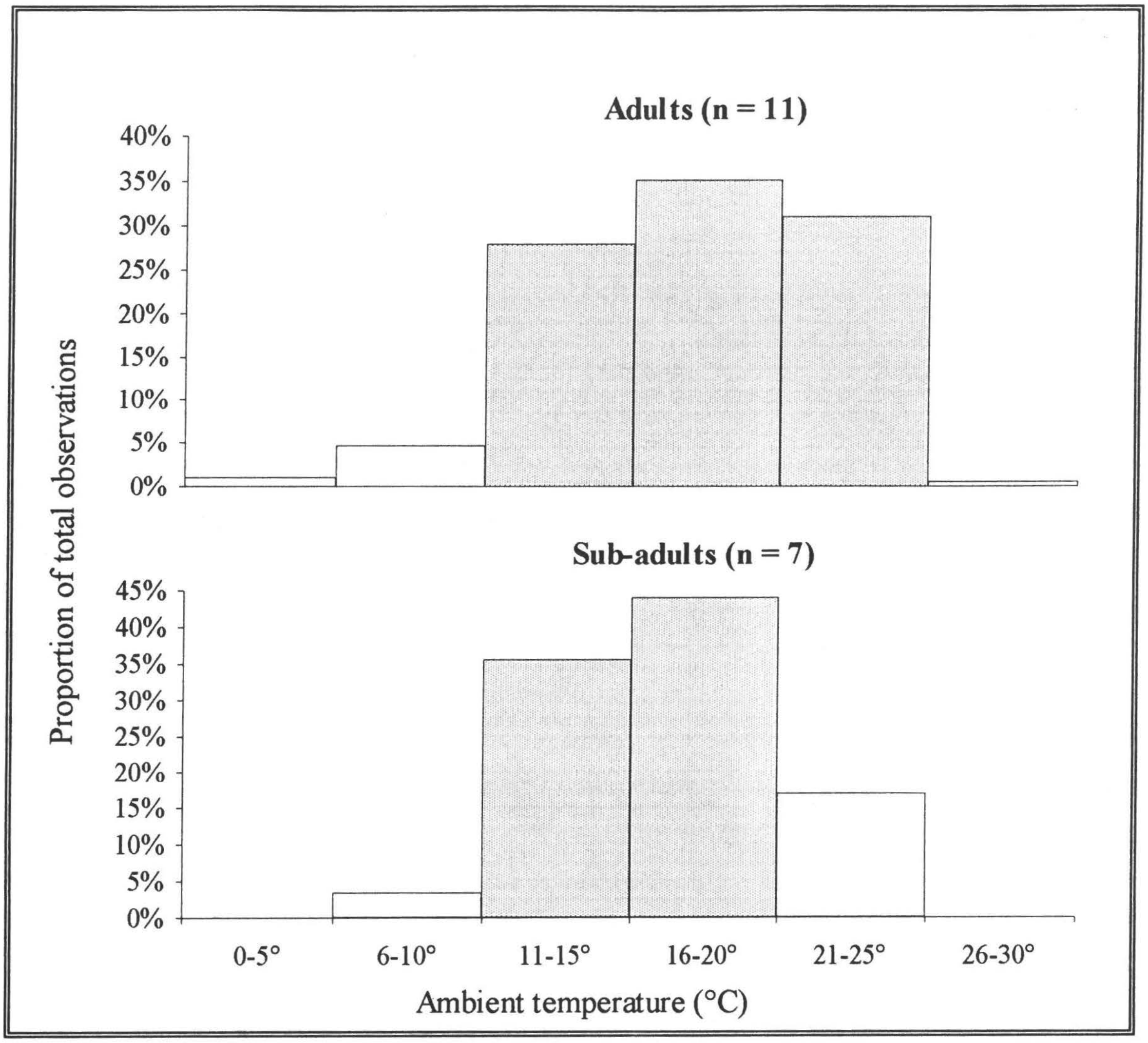


**Fig. 4.5.** Temperature range of activity for adult and sub-adult pangolins expressed as a percentage of total observations. Shaded regions represent their preferred temperature range of activity. The temperature range for sub-adults is from data accumulated during winter only.

Temperature appeared to have a moderate affect on the activity of pangolins during winter (Fig. 4.6), whereas during summer it appeared to have no affect. There was a moderate but not significant correlation between the mean time that pangolins left their dens during the winter months and the mean monthly temperature recorded at 20h00 at Skukuza weather station between June 1993 and July 1994 (Fig. 4.6; $r = 0.57$, $df = 5$, $P < 0.18$). In addition, the correlation between the mean time that pangolins returned to their dens during winter and the mean monthly temperature at 20h00 was not significant ($r = -0.22$, $df = 5$, $P > 0.6$).

Interestingly, humidity appeared to have a greater effect than temperature on pangolin activity during summer. This statement is supported by the significant negative correlation between the mean monthly relative humidity and the time that pangolins returned to their dens during summer ($r = -0.84$, $df = 6$, $P < 0.007$; Fig. 4.7).

## Diet

The diet of 11 pangolins was recorded over a period of 14 months (June 1993 - July 1994) and a total of 4698 feeding bouts was observed. Of the 50 ant species and five termite species identified in the study area during this period, only 15 ant species and five termite species were preyed on by pangolins.

The number of ant and termite species preyed on by pangolins over the period of 14 months varied considerably from one month to the next. The largest number of species was preyed on during September to November 1993 and the largest number of species caught in pitfall traps was during the period March to June 1994 (Fig. 4.8). Thus, the number of species preyed on by pangolins did not

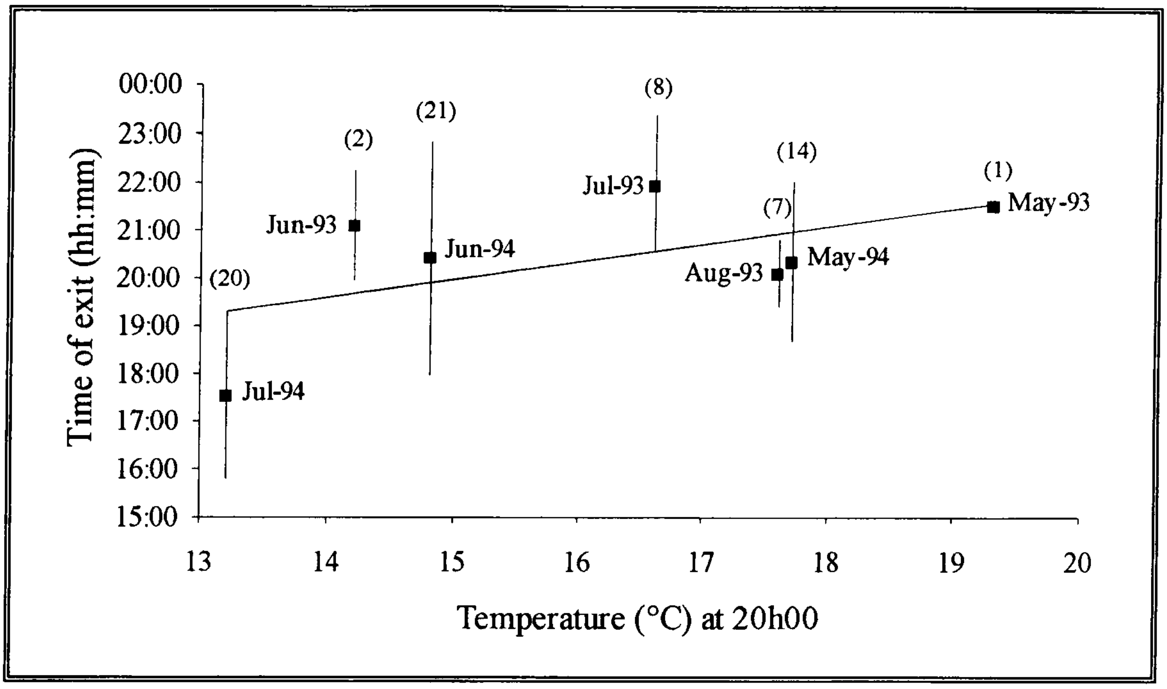


**Fig. 4.6.** A linear regression of the time that adult pangolins were observed leaving their dens during the winter months as a function of the mean monthly temperature recorded at 20h00 ($r^2 = 0.32$, $F_{(1,5)} = 2.40$, df = 5, $P < 0.18$).

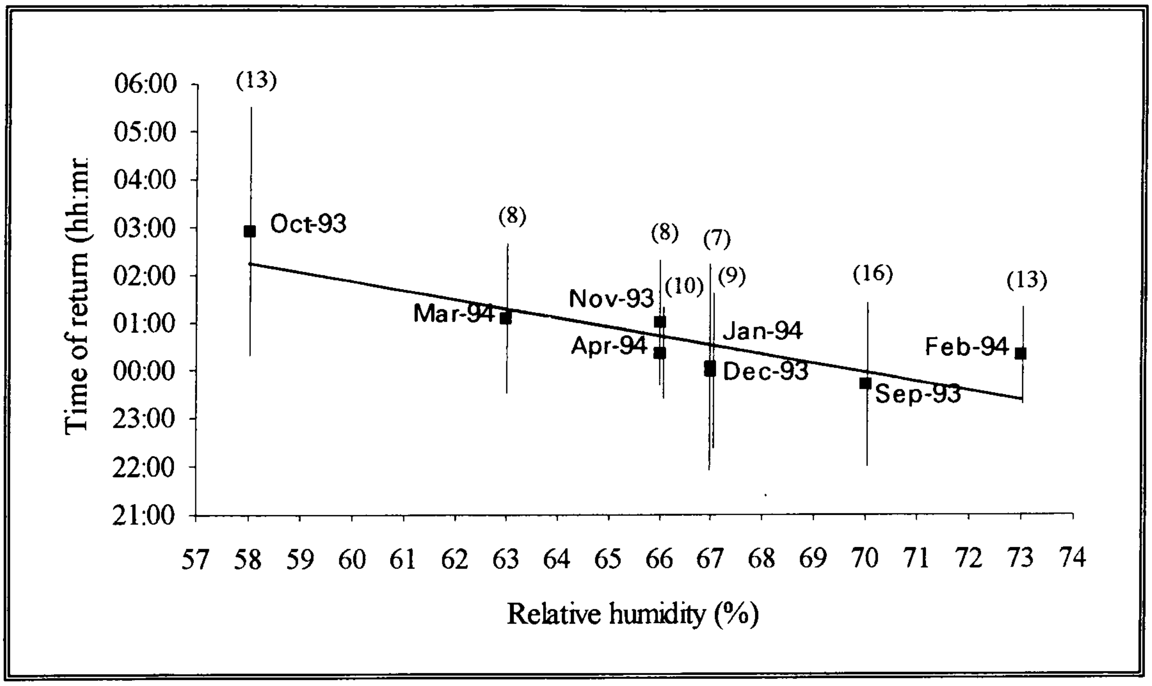


**Fig. 4.7.** A linear regression of the time pangolins were observed returning to their dens during the summer months as a function of the mean monthly humidity ($r^2 = 0.71$, $F_{(1,6)} = 14.90$, df = 6, $P < 0.007$).

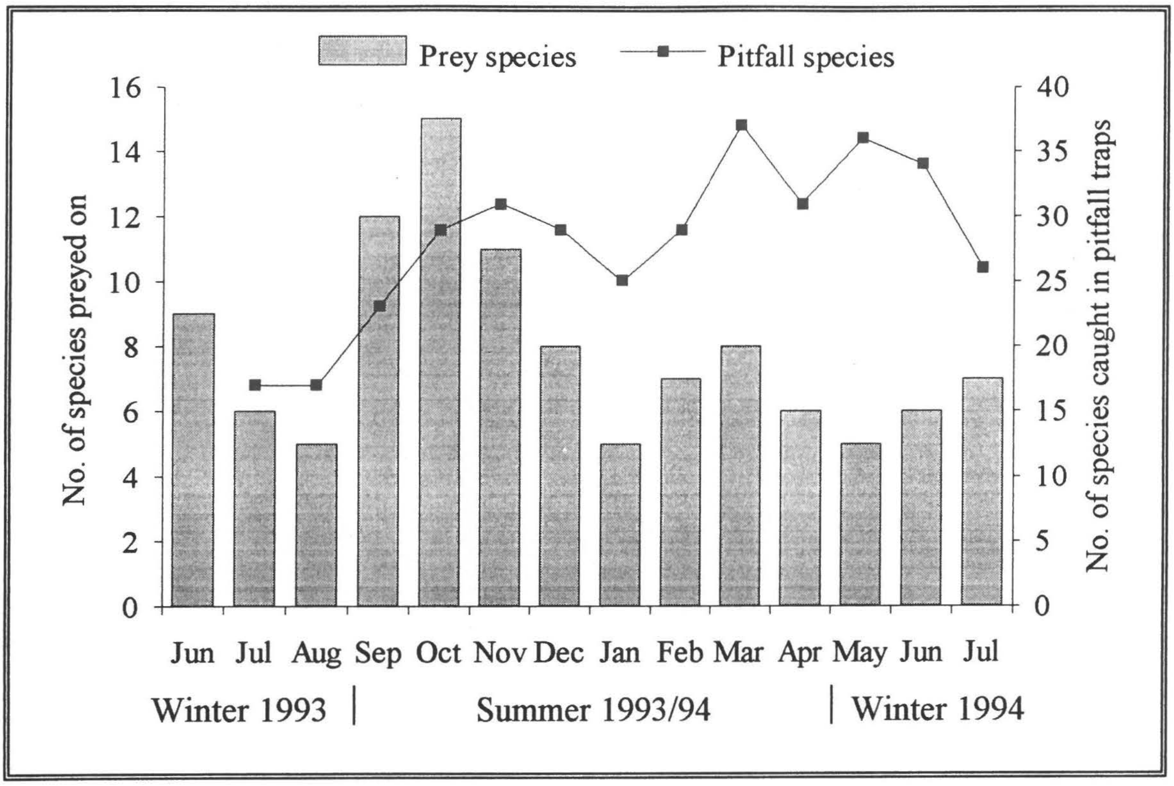


**Fig. 4.8.** The seasonal variation of the number of ant and termite species preyed on by pangolins compared with the number caught in pitfall traps (r = 0.08, df = 11, $P > 0.7$).

coincide with the number caught in pitfall traps and there appeared to be no correlation between these (r = 0.08, df = 11, *P* > 0.7).

The relative importance (RI) of the various prey species in the pangolin's diet is given in table 4.3. The RI was calculated as the proportion of time pangolins spent feeding on each species. The relative importance of the ants (Formicidae) in the pangolin's diet was 96.7% whereas the termites (Isoptera) constituted only 3.3%. The most important prey species in their diet was the ant species *A. custodiens* with an RI value of 77.3%. Only six of the 19 species (five ants and one termite) constituted 97.7% of the pangolin's diet and the seasonal variation in the composition of these species in their diet is illustrated in Fig. 4.9.

While the RI of *A. custodiens* as a prey species decreased from 83% during winter to 72% during summer, the RI of *M. natalensis* increased eight fold from 2% to 16% (Fig. 4.9). The ant species *P. schistacea* was also preyed on considerably more during summer, particularly during February 1994 when the RI of this species was 19% (Fig. 4.9). In contrast, the two species *C. cinctellus* and *H. mossambicus* were preyed on more during winter (Fig. 4.9). The RI of *C. cinctellus* in the pangolin's diet was low for most the year, however, this species contributed substantially towards their diet during July 1994 when its RI reached 40% (Fig. 4.9). Similarly, the RI of *Camponotus* sp.- *maculatus*-group was also low for most of the year except during September 1993 when it reached 18% (Fig. 4.9).

*H. mossambicus* was the only termite species that made a significant contribution to the pangolin's diet. This species was only preyed on when they were active in their connecting galleries and entrance ports at the soil surface

**Table 4.3.** The total time pangolins spent feeding on the various species of ants and termites, and their relative importance in the pangolin's diet.

| Ant and termite species | Total feeding time (s) | Total feeding bouts | Relative importance in diet (%) | Mean feed time per bout (s) ±SD |
|---|---|---|---|---|
| *Aenictus eugenii* | 6 | 1 | < 0.1 | 6.0 ±0 |
| *Pheidole* sp. 3 | 25 | 2 | < 0.1 | 12.5 ±4.5 |
| *Tetramorium longicorne* | 40 | 2 | < 0.1 | 20.0 ±10 |
| *Crematogaster* sp.- *castanea*-group | 53 | 2 | < 0.1 | 26.5 ±1.5 |
| *Ocymyrmex fortior* | 58 | 2 | < 0.1 | 29.0 ±9 |
| *Tetramorium weitzeckeri* | 59 | 1 | < 0.1 | 59.0 ±0 |
| *Rhadinotermes coarctatus** | 99 | 2 | 0.1 | 49.5 ±38.5 |
| *Dorylus badius* | 215 | 2 | 0.1 | 107.5 ±38.5 |
| Termitidae* | 281 | 12 | 0.1 | 23.4 ±16.9 |
| *Trinervitermes rapulum** | 319 | 3 | 0.2 | 106.3 ±116.3 |
| *Camponotus congolensis* | 685 | 13 | 0.4 | 52.7 ±37.6 |
| *Pheidole* sp. 2 | 741 | 13 | 0.4 | 57.0 ±56.9 |
| *Monomorium junodi* | 749 | 11 | 0.4 | 68.1 ±46.6 |
| *Odontotermes* sp. * | 1034 | 45 | 0.6 | 23.0 ±29.4 |
| *Camponotus* sp.- *maculatus*-group | 2739 | 60 | 1.5 | 45.7 ±38.7 |
| *Hodotermes mossambicus** | 4517 | 529 | 2.4 | 8.5 ±7.7 |
| *Polyrhachis schistacea* | 5251 | 77 | 2.8 | 68.2 ±62.8 |
| *Camponotus cinctellus* | 8893 | 178 | 4.7 | 50.0 ±39.6 |
| *Myrmicaria natalensis* | 16878 | 187 | 9.0 | 90.3 ±121.1 |
| *Anoplolepis custodiens* | 144373 | 3530 | 77.2 | 40.9 ±33.4 |
| TOTALS | 187015 | 4672 | 100.0 | 40.0 ±43.1 |

* Termite species

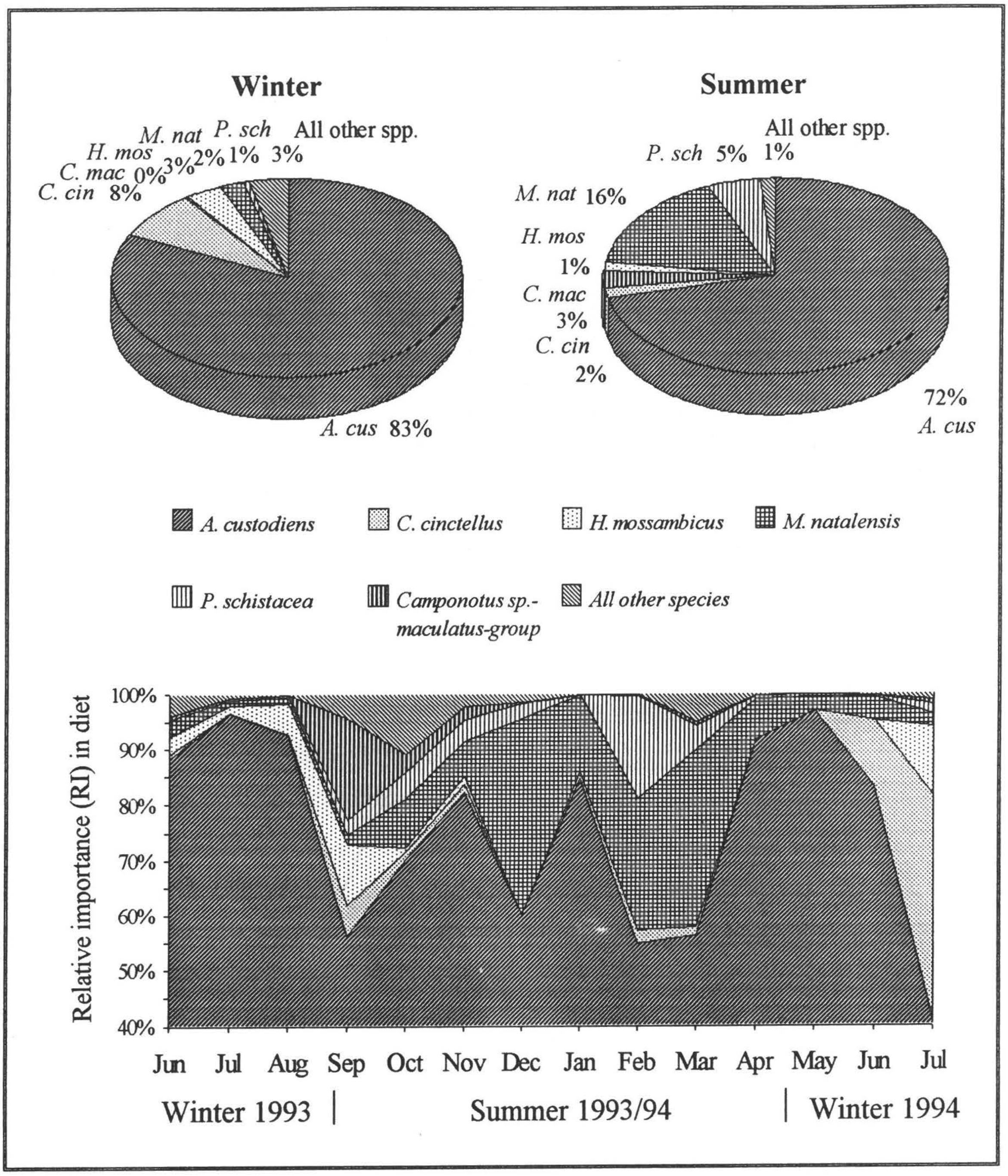


**Fig. 4.9.** The seasonal variation in the composition of the six most important prey species occurring in the pangolins diet over a period of 14 months.

(pers. obs.). This was usually during winter and 71% of the observed feeding bouts on *H. mossambicus* were also during winter (Fig. 4.9).

The feeding frequency (number of feedings per hour) of pangolins appears to be inversely related to the number of ant and termite prey species that were active above ground (Spearmans rank correlation coefficient; $r_S = -0.81$, $n = 13$, $P < 0.001$; Fig 4.10). Thus an increase in the activity of the pangolin's prey appears to decrease their feeding frequency. This is particularly pronounced by the above ground activity of *A. custodiens*. During February and March '94, when the activity of *A. custodiens* was the highest, the overall frequency of feedings by pangolins was the lowest (Fig. 4.11). In addition, the feeding frequency of pangolins on *A. custodiens* and *H. mossambicus* appear to be inversely related. This is depicted by the lower feeding frequency on *A. custodiens*, especially during August '93, September '93 and July '94 when the frequency of feedings on *H. mossambicus* was relatively high (Fig. 4.11).

## Foraging behaviour

After pangolins left their dens in the evening they foraged in a small area, usually within a 500 m radius of the den. While foraging they moved between several feeding sites, which are small areas of approximately 400m² where they would search for and feed on their ant and termite prey. Once they completed their foraging excursion they either returned to the same den or another den within a few kilometres. Three foraging patterns manifested by pangolins were identified during these foraging excursions:

a) ***Directional foraging*** (Fig. 4.12a)

This foraging pattern was usually exhibited when pangolins vacated one den to move to a new den, so that the general direction that they moved between feeding sites was towards a new den. Thus, directional foraging

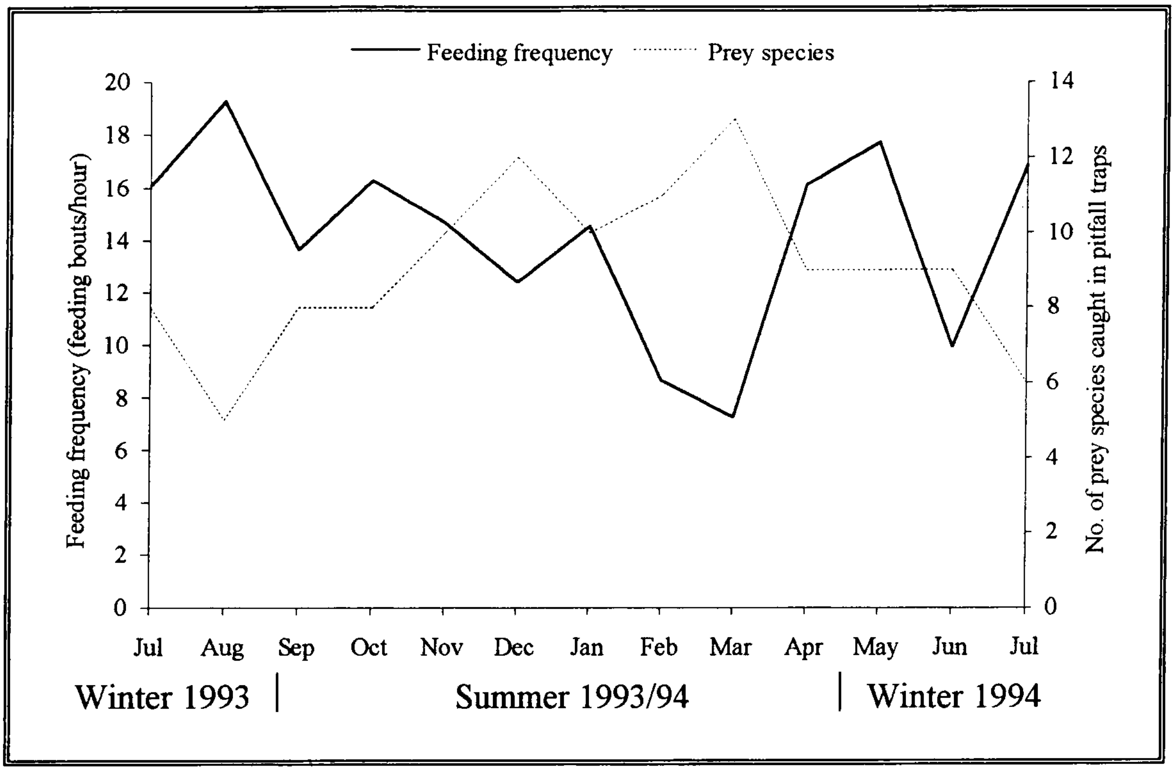


**Fig. 4.10.** The seasonal variation of the mean feeding frequency of pangolins recorded for each month, in relation to the mean number of prey species caught in pitfall traps ($r_S = -0.81$, $n = 13$, $P < 0.001$).

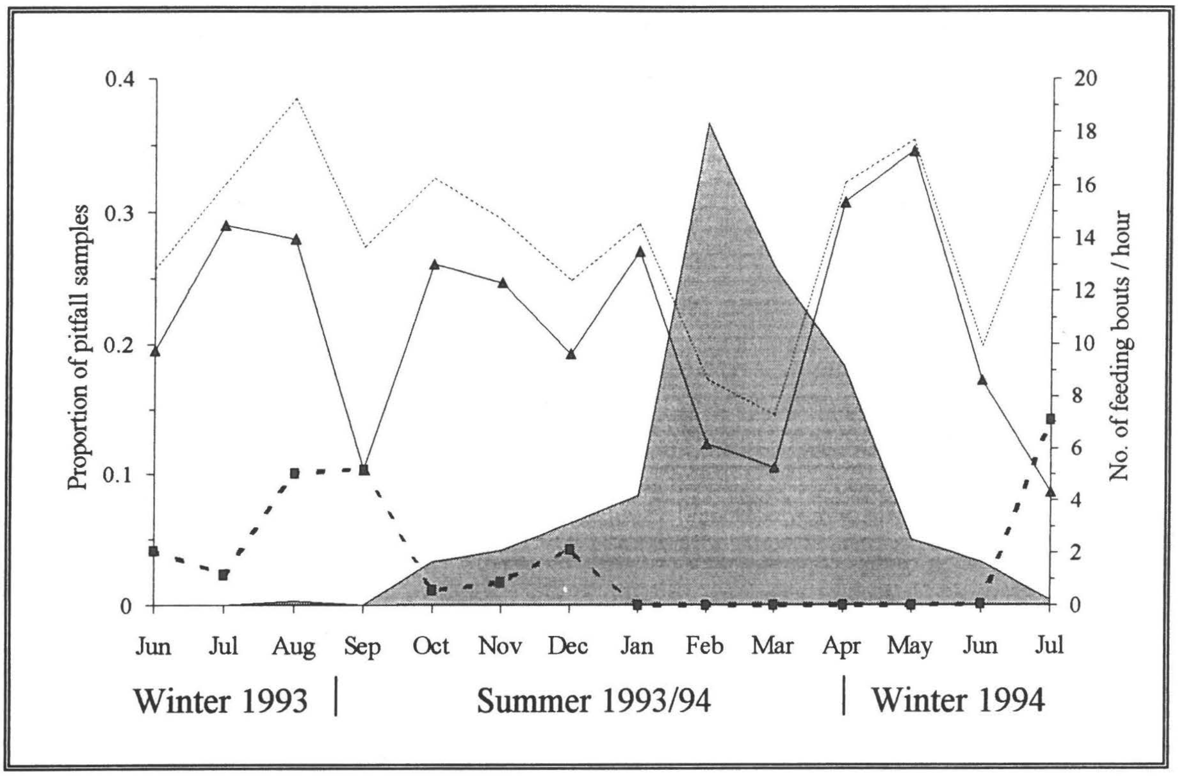
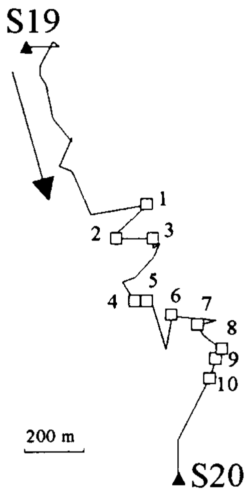


**Fig. 4.11.** The seasonal variation of feeding frequency of pangolins on *A. custodiens* (—▲—) and *H. mossambicus* ( - - ■ - ). This is compared with the pangolin's overall feeding frequency (------) and the activity of *A. custodiens* (▨). Activity of *A. custodiens* = $p_i/\Sigma p_i$ where $p_i$ = the proportion of pitfall samples where species *i* was found.

## (a) DIRECTIONAL FORAGING

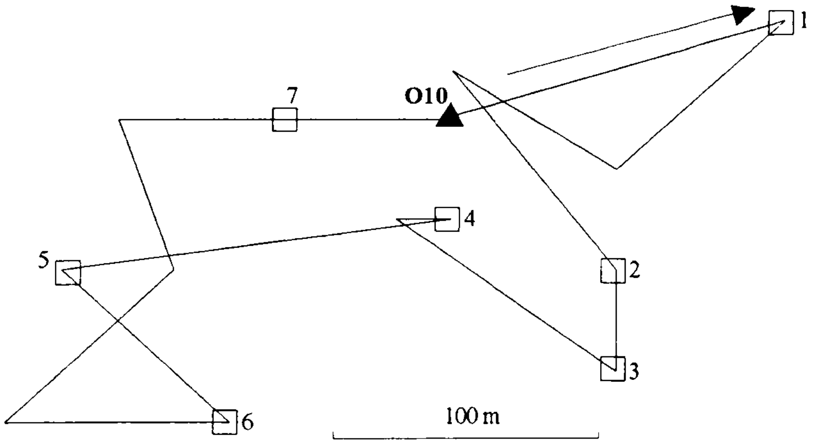
**17/02/1994 - Shumi; 20h48-01h45**



| Feeding site number | Number of feeding bouts | Total feeding time (min) | Mean dist. between bouts (m) |
|---|---|---|---|
| 1 | 3 | 1.8 | 14 |
| 2 | 1 | 0.6 | 0 |
| 3 | 1 | 1.6 | 0 |
| 4 | 1 | 1.8 | 0 |
| 5 | 2 | 2.1 | 10 |
| 6 | 1 | 0.8 | 0 |
| 7 | 1 | 1.4 | 0 |
| 8 | 1 | 3.8 | 0 |
| 9 | 5 | 4.4 | 7 |
| 10 | 6 | 4.7 | 2 |

## (b) NON-DIRECTIONAL FORAGING

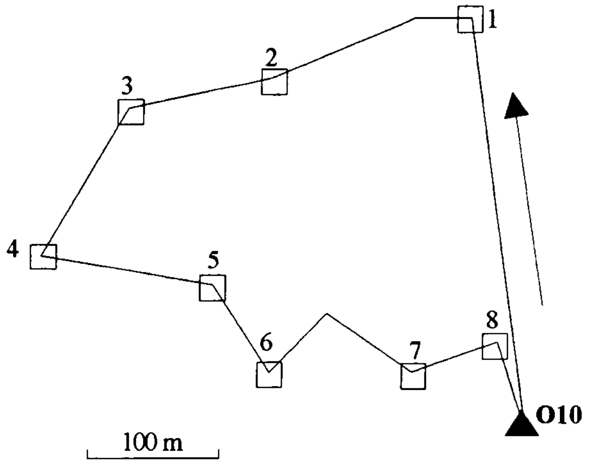
**21/11/1994 - Ozela; 19h05-23h41**



| Feeding site number | Number of feeding bouts | Total feeding time (min) | Mean dist. between bouts (m) |
|---|---|---|---|
| 1 | 6 | 4.3 | 4 |
| 2 | 2 | 2.4 | 2 |
| 3 | 3 | 2.4 | 5 |
| 4 | 1 | 1.5 | 0 |
| 5 | 2 | 9.2 | 16 |
| 6 | 5 | 6.2 | 0 |
| 7 | 1 | 0.9 | 0 |

## (c) CIRCULAR FORAGING

**20/11/1993 - Ozela; 20h09-00h59.**



| Feeding site number | Number of feeding bouts | Total feeding time (min) | Mean dist. between bouts (m) |
|---|---|---|---|
| 1 | 3 | 2.3 | 3 |
| 2 | 17 | 8.5 | 2 |
| 3 | 28 | 13.9 | 4 |
| 4 | 28 | 20.4 | 4 |
| 5 | 32 | 14.3 | 1 |
| 6 | 5 | 2.8 | 7 |
| 7 | 1 | 0.2 | 0 |
| 8 | 1 | 0.1 | 0 |

**Fig. 4.12a - 4.12c.** Example of three typical patterns of pangolins foraging activities during evening excursions. The squares represent feeding sites and the arrows indicate the direction the pangolin walked after leaving the den (indicated by triangles).

appeared to indicate a pangolin's intention of moving from one destination to another on a relatively straight course.

b) ***Non-directional foraging*** (Fig. 4.12b)

Unlike directional foraging this foraging pattern was a haphazard zigzagging movement between feeding sites and within feeding sites. This was a method used by pangolins to search for the nests of their ant and termite prey.

c) ***Circular foraging*** (Fig. 4.12c)

This foraging pattern has components of both directional foraging and non-directional foraging. The directional component was evident when the pangolins travelled between feeding sites, since their direction of movement was in a relatively straight line. The non-directional component was evident within the feeding sites and occasionally between feeding sites when the pangolins were haphazardly searching for prey. However, the general direction of foraging was a circular route beginning when pangolins left their den until the time they returned.

A total of 331.6 hours of data on feeding behaviour was recorded during 375 observation periods. The number of feeding bouts recorded each evening and the distances between these feedings varied considerably depending on the amount of prey that the pangolins were locating. There was a significant negative correlation between the mean number of feeding bouts per hour and the mean distance between feedings recorded each month ($r = -0.67$, $df = 12$, $P < 0.01$; Fig. 4.13). There was also a significant correlation between the mean duration of feeding bouts and the mean distance between feedings recorded each month ($r = 0.78$, $df = 12$, $P < 0.002$; Fig. 4.14). Thus both the number of feeding bouts and the duration of these feedings appeared dependent on the distances between them. Interestingly, the mean distance between feeding bouts recorded each

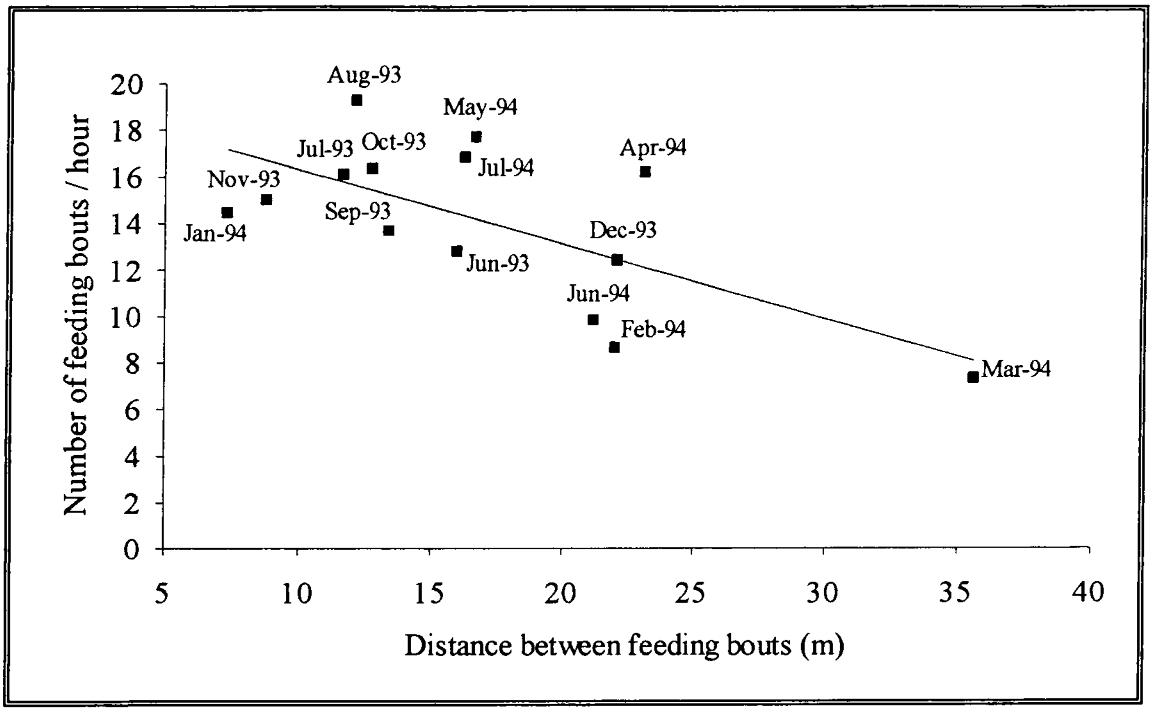


**Fig. 4.13.** A linear regression of the mean number of feeding bouts observed each hour as a function of the mean distance between each feeding ($r^2 = 0.45$, $F_{(1,12)} = 9.76$, df = 12, $P < 0.01$).

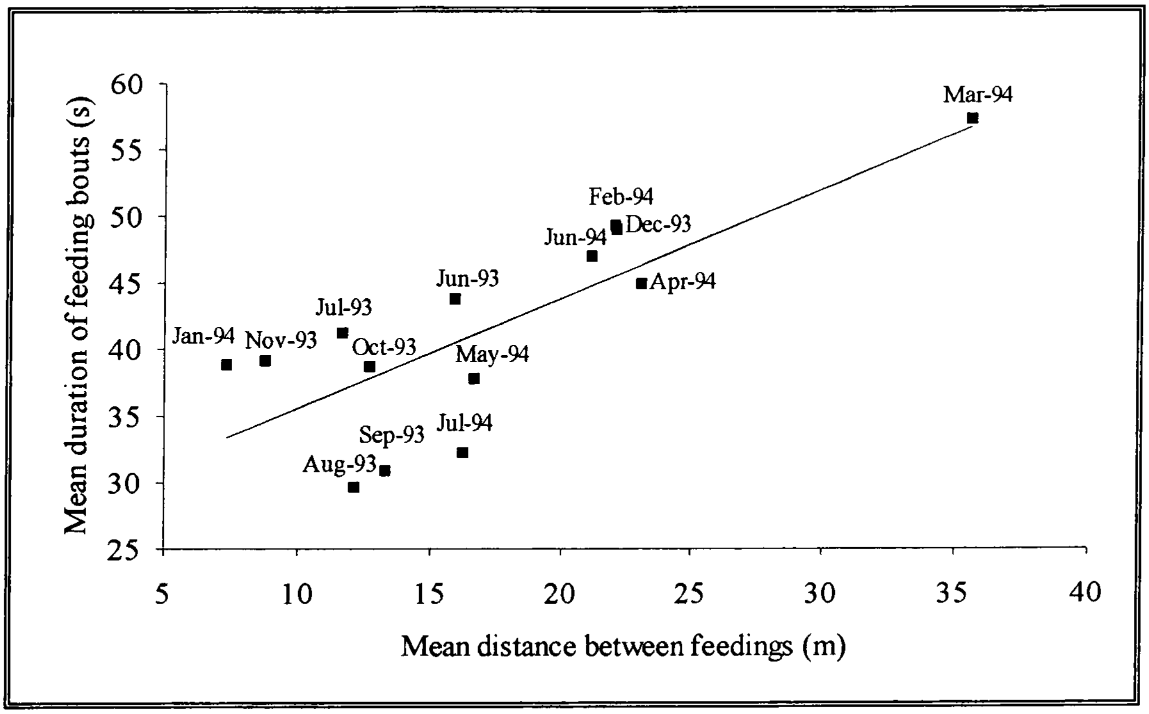


**Fig. 4.14.** A linear regression of the average duration of each feeding as a function of the mean distance between feeding bouts ($r^2 = 0.6$, $F_{(1,12)} = 18.15$, df = 12, $P < 0.002$).

month during winter was 15.2 m (SD = 43.7m) whereas during summer it was 17.3 m (SD = 40.5 m) and this difference between winter and summer was significant ($t = -1.72$, df = 4605, $P < 0.05$).

Although most of the pangolin's activity period was devoted to foraging for ants and termites, only 15.7% of this time was spent actually feeding. Pangolins sniff the ground continuously while searching for prey. When they locate an aggregation of ants or termites their sniffing intensity increases and the underground galleries are then quickly opened with the front claws followed by a rapid insertion of the long rod-shaped tongue. The duration of these feeding bouts is very short with an overall mean duration per feeding bout of only 40 sec (S.D. = 43.1; range = 2 - 1198; n = 4672) and a mode of 15 seconds. Of the 4672 feeding bouts recorded, 13.6% were less than 10 sec, 32.5% were less than 20 sec, 81% were less than a minute and 96.2% were less than two minutes. The number of feeding bouts, the time pangolins spent feeding and the mean duration of each feeding bout is listed for each species preyed on by the pangolins in Table 4.3.

Of the 4672 feeding bouts recorded 4633 (99%) were on ants and termites situated below the soil surface. The remaining 1% were from animal dung, the soil surface and dead twigs or logs. The majority of feeding bouts were from ground digs that accounted for 3299 (71%) while 1334 (28%), also a large proportion, were from active ant or termite ports that open at the soil surface. Interestingly the duration of feeding bouts was considerably shorter when pangolins fed directly from an active port compared to when they fed from a ground dig ($t = -19.95$; df = 4631; $p < 0.001$) (cf. Table 4.4 & 4.5). A comparison between the duration of feeding bouts from ground digs and active

**Table 4.4.** Mean duration of feeding bouts recorded for each pangolin, while feeding directly out of an active ant or termite port.

| Name | Total No. of port feedings | Proportion of feeding bouts (%) | Mean duration of feeding bouts (s) ±SD | No. of species preyed |
|---|---|---|---|---|
| **Males** | | | | |
| Jobu | 264 | 27 | 22 ± 18 | 6 |
| Shumi | 196 | 24 | 27 ± 33 | 3 |
| Zinga | 11 | 23 | 16 ± 17 | 2 |
| **Females** | | | | |
| Nina | 278 | 31 | 15 ± 19 | 6 |
| Ozela | 241 | 32 | 24 ± 24 | 6 |
| Yela | 107 | 32 | 17 ± 15 | 7 |
| Vunga | 58 | 28 | 25 ± 16 | 6 |
| Penula | 13 | 52 | 38 ± 30 | 2 |
| Azana | 9 | 64 | 21 ± 17 | 1 |
| **Sub-adult** | | | | |
| Imini | 157 | 29 | 17 ± 18 | 4 |
| Totals | 1334 | 28 | 21 ± 22 | 10 |

**Table 4.5.** The correlation coefficient (r) for the mean duration of feeding bouts vs. mean dig depth, calculated for all ant or termite species preyed on by each pangolin.

| Name | Total number of digs | Mean duration of feeding bouts (s) ±SD | No. of species preyed | Mean duration of feeding bouts (s) vs Mean dig depth (cm) r | df | p |
|---|---|---|---|---|---|---|
| **Males** | | | | | | |
| Jobu | 728 | 43 ± 31 | 7 | 0.83 | 5 | $< 0.05$ |
| Shumi | 615 | 50 ± 37 | 8 | 0.8 | 6 | $< 0.05$ |
| Zinga | 38 | 53 ± 37 | 1 | - | - | - |
| Zimu | 4 | 184 ± 132 | 1 | - | - | - |
| **Females** | | | | | | |
| Nina | 608 | 43 ± 39 | 10 | 0.93 | 8 | $< 0.001$ |
| Ozela | 504 | 52 ± 77 | 9 | 0.84 | 7 | $< 0.01$ |
| Yela | 229 | 35 ± 28 | 7 | 0.93 | 5 | $< 0.01$ |
| Vunga | 152 | 57 ± 61 | 4 | 0.99 | 2 | $< 0.001$ |
| Penula | 12 | 57 ± 19 | 1 | - | - | - |
| Lola | 9 | 52 ± 31 | 2 | - | - | - |
| Azana | 5 | 15 ± 9 | 1 | - | - | - |
| Thamo | 2 | 107 ± 74 | 1 | - | - | - |
| **Sub-adult** | | | | | | |
| Imini | 393 | 56 ± 42 | 9 | 0.32 | 7 | $> 0.1$* |
| Totals | 3299 | 48 ± 47 | 20 | 0.59 | 17 | $< 0.01$ |

* Not significant

ports when pangolins preyed on the six most important species in its diet is also illustrated in Fig. 4.15.

A seasonal variation in the duration of feeding bouts was also evident since feedings from both ground digs and active ports were shorter during winter. The mean duration of feeding bouts from ground digs of 46.4 sec (S.D. = 37.6 sec) during winter was shorter than the 48.9 sec (S.D. = 55.1 sec) recorded during summer, however the difference was not significant ($t = -1.52$; df = 3337; $p < 0.07$). Similarly, the mean duration of feeding bouts from active ports of 18.3 sec (S.D. = 37.6 sec) during winter was significantly shorter than the 24.2 sec (S.D. = 55.1 sec) during summer ($t = -4.90$; df = 1333; $p < 0.001$).

The mean depth of the holes excavated by pangolins, and the mean time they spent digging before feeding on the various species of ants and termites is listed in Table 4.6. The overall mean dig depth was 3.8 cm (S.D. = 2.5 cm) and the mean dig time was 8.7 sec (S.D. = 9.5 sec). There was a significant correlation between the mean dig time and the mean dig depth of the holes excavated when pangolins preyed on each species of ant and termite ($r = 0.665$, df = 17, $P < 0.01$). Thus the amount of effort they put into exposing their prey corresponded with the depth that the species they were feeding on could be located below the soil surface.

Of the ant and termite species that were recorded in at least 10 ground digs, the mean depth of the holes excavated to expose the ant species *M. natalensis* was the deepest whereas the shallowest digs were recorded for the termite species *H. mossambicus* (Table 4.6). A mean dig depth of 6.6 cm (S.D. = 4.2 cm) was recorded for *M. natalensis* and a mean depth of 1.3 cm (S.D. = 0.5 cm) for *H. mossambicus*. Interestingly, the duration of feeding bouts on each species

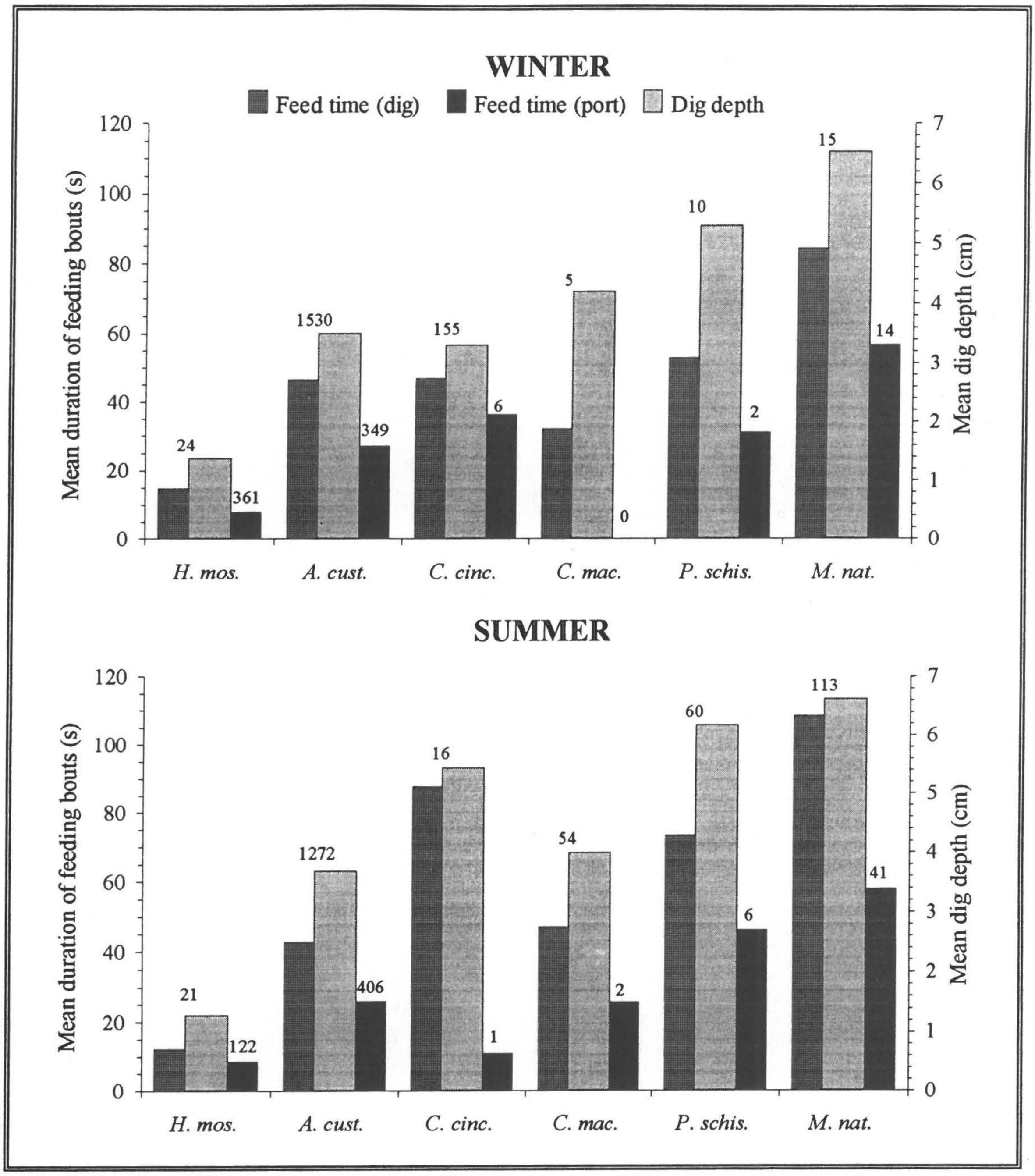


**Fig. 4.15.** The feeding behaviour of 11 pangolins during winter and 10 pangolins during summer, depicting a comparison between the feeding bouts on their six most important prey species. Feed time (dig) = feeding bouts from a hole excavated in the ground, dig depth = the depth of the excavated hole, and feed time (port) = feeding bouts from an active ant or termite port. Numbers above the respective columns represents the number of feeding bouts recorded.

**Table 4.6.** The mean depth of the holes excavated in the ground when pangolins preyed on the various species of ants and termites.

| Ant and termite species | Total ground digs | Total dig time (s) | Mean dig time (s) ±SD | Mean dig depth (cm) ±SD |
|---|---|---|---|---|
| *Aenictus eugenii* | 1 | 5 | 5.0 ±0 | 1.0 ±0 |
| *Crematogaster* sp.- *castanea*-group | 1 | 10 | 10.0 ±0 | 7.0 ±0 |
| *Rhadinotermes coarctatus** | 1 | 25 | 25.0 ±0 | 10.0 ±0 |
| *Tetramorium weitzeckeri* | 1 | 5 | 5.0 ±0 | 4.0 ±0 |
| *Dorylus badius* | 2 | 15 | 7.5 ±2.5 | 4.5 ±0.5 |
| *Ocymyrmex fortior* | 2 | 90 | 45.0 ±10 | 7.5 ±0.5 |
| *Pheidole* sp. 3 | 2 | 15 | 7.5 ±2.5 | 4.0 ±1 |
| *Tetramorium longicorne* | 2 | 15 | 7.5 ±2.5 | 3.0 ±2 |
| Termitidae* | 4 | 35 | 8.8 ±4.2 | 2.5 ±1.1 |
| *Odontotermes* sp.* | 10 | 75 | 7.5 ±4.6 | 1.9 ±1.3 |
| *Monomorium junodi* | 11 | 290 | 26.4 ±19.7 | 5.6 ±2.7 |
| *Pheidole* sp. 2 | 11 | 205 | 18.6 ±14 | 4.6 ±2.7 |
| *Camponotus congolensis* | 13 | 160 | 12.3 ±8.5 | 4.5 ±2.0 |
| *Hodotermes mossambicus** | 46 | 230 | 5.0 ±0 | 1.3 ±0.5 |
| *Camponotus* sp.- *maculatus*-group | 58 | 535 | 9.2 ±8.4 | 4.1 ±2.5 |
| *Polyrhachis schistacea* | 69 | 675 | 9.6 ±7.8 | 6.1 ±3.7 |
| *Myrmicaria natalensis* | 128 | 2000 | 15.4 ±26.6 | 6.6 ±4.2 |
| *Camponotus cinctellus* | 171 | 1425 | 8.3 ±6.2 | 3.5 ±1.9 |
| *Anoplolepis custodiens* | 2766 | 23050 | 8.3 ±7.8 | 3.6 ±2.2 |
| TOTALS | 3299 | 28860 | 8.7 ±9.5 | 3.8 ±2.5 |

* Termite species

preyed on appeared dependent on the depth that these species were located below the soil surface since those species that were preyed on from deeper digs were also preyed on for longer during each feeding (Fig. 4.15). Consequently a highly significant interspecies correlation existed between the mean duration of feeding bouts and the mean depth of the diggings required to expose the various species of ants and termites (Fig. 4.16; $r = 0.95$, $df = 8$, $P < 0.001$). The above correlation was also significant for each study animal except for the sub-adult pangolin, Imini (Table 4.5).

There was a significant overall seasonal variation in the mean depth of the feeding digs which were deeper during summer than during winter ($t = 6.1$, $df = 3337$, $P < 0.001$). The mean dig depth during summer was 4.0 cm (S.D. = 2.8 cm) whereas during winter it was 3.5 cm (S.D. = 2.0 cm). The depth of the ground digs appeared to be influenced by rainfall since there was a moderate correlation between the mean monthly rainfall and the mean depth of ground digs recorded each month, however, this was not significant (Spearmans rank correlation coefficient; $r_s = 0.45$, $n = 14$, $P < 0.1$). The mean dig depth was the deepest during March and April 1994, towards the end of the rainy season when the soil was softened from the season's rainfall (Fig. 4.17).

Pangolins occasionally preyed on the egg, larvae and pupal (ELP) stages of ants, however, they were never observed preying on the alates of ants or the alates and ELP stages of termites. Although pangolins preyed on the adult stages of 19 species of ants and termites, they were observed preying on ELP stages of only five species. In addition, the ELP stages of ants were preyed on almost exclusively during summer and only one of the 87 records was during winter (Fig. 4.18).

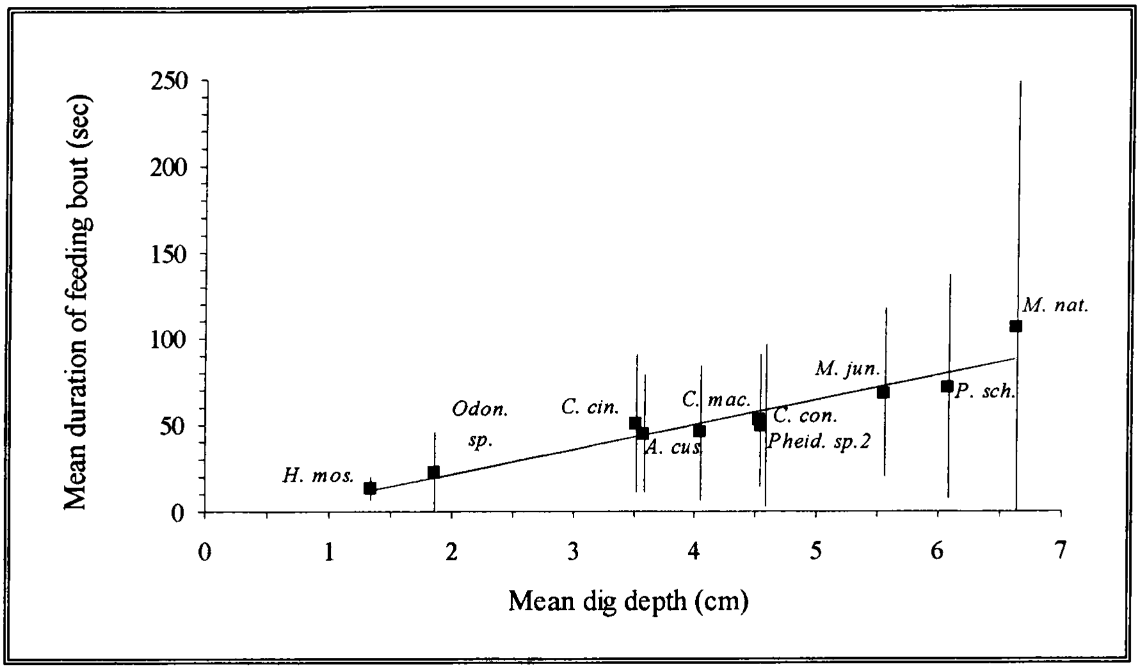


**Fig. 4.16.** A linear regression of the mean duration of feeding bouts as a function of the mean depth of the hole excavated by pangolins while feeding on eight species of ants and two species of termites ($r^2 = 0.9$, $F_{(1,8)} = 68.8$, df = 8, $P < 0.001$). Only species that were recorded in more than 10 feeding bouts were used for the regression.

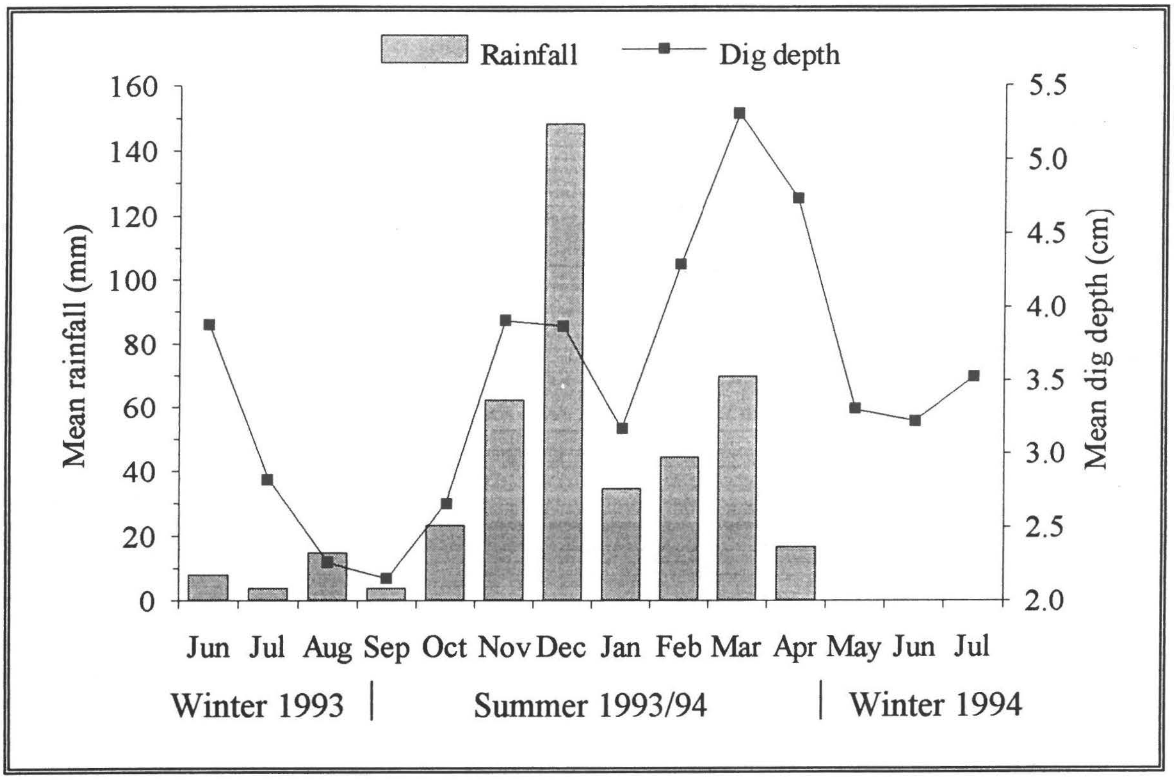


**Fig. 4.17.** The seasonal variation of the mean monthly rainfall and the mean depth pangolins were recorded digging for prey while foraging.

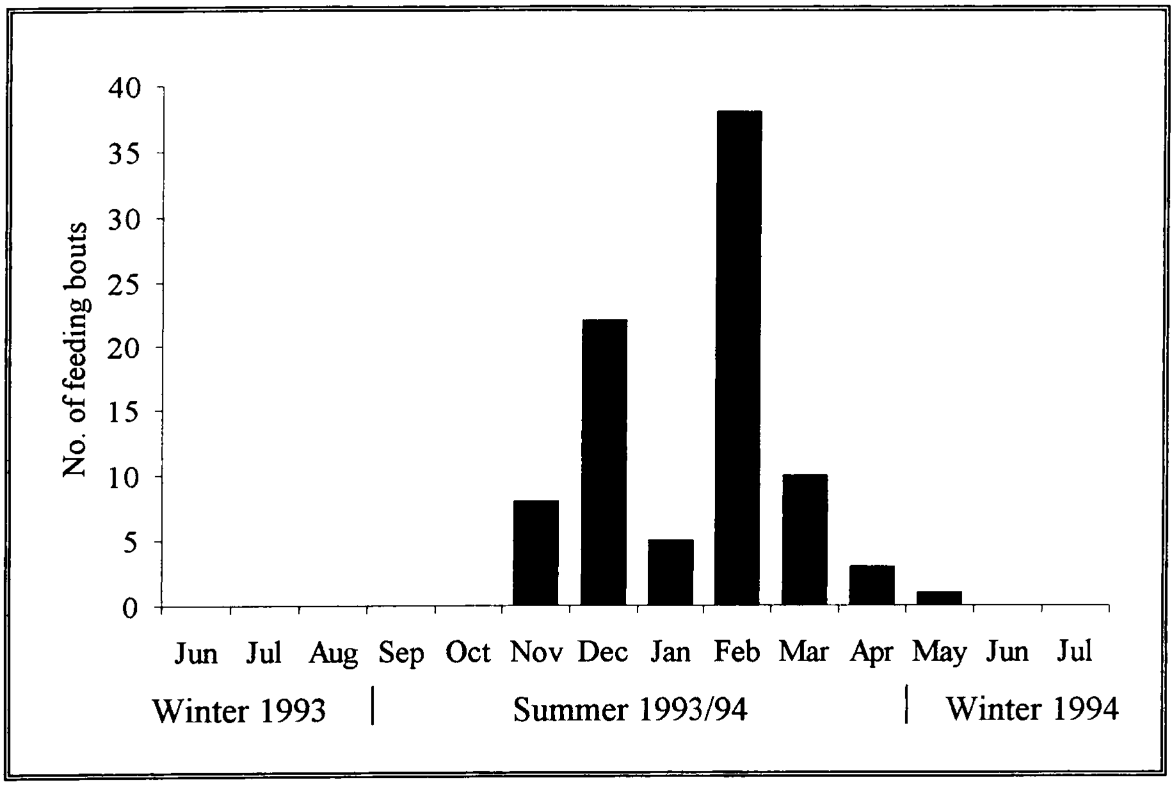


**Fig. 4.18.** Seasonal variation in the total number of feedings recorded on egg, larvae and pupal stages of ants.

A total of 87 feeding bouts were recorded on ELP stages, a mere 1.9% of the total feeding bouts, and 85 (97.7%) of observations were on the three species *A. custodiens, M. natalensis* and *P. schistacea* (Table 4.7). Interestingly, the proportion of feeding bouts on ELP stages of *A. custodiens* was almost negligible (0.7%), whereas 18% of *M. natalensis* and 35% of *P. schistacea* were on ELP stages.

The majority of feeding bouts on ELP stages were from ground digs which accounted for 92% of feedings while the remaining 8% were from port feeds (Table 4.7). No feedings were recorded on ELP stages of *A. custodiens* from an active port. The mean duration of feedings from ELP stages was significantly longer than from adult stages (Two sample t-test assuming unequal variances; $t = 3.6$, $df = 85.2$, $n = 4672$, $P < 0.001$). The mean duration of feeding bouts from ELP stages was 101 sec. (S.D. = 161 sec.) whereas from adult stages it was only 39 sec. (S.D. = 37 sec.). Longer feeding bouts were also recorded from both ground digs and port feeds when pangolins preyed on ELP stages (Table 4.7; Fig. 4.18).

## DISCUSSION

### Activity

The activity of Cape pangolins is generally regarded as being nocturnal and to a lesser degree diurnal (Dorst & Dandelot 1970; Kingdon 1971; Smithers 1983). In contrast, Jacobsen *et al.* (1991) reported pangolins as being mainly crepuscular since 56% of replies to a survey from incidental observers in the Transvaal indicated a high frequency of activity between 16h00 and 18h00. His findings were in accordance with a similar survey conducted by Coulson (1989) in

**Table 4.7.** A comparison between the feeding bouts on egg, larvae and pupal (ELP) stages, and adult stages of three ant species.

| | Feeding bouts on ELP stages | | | Feeding bouts on adult stages | | |
|---|---|---|---|---|---|---|
| | Mean feed time (s) ±SD | Mean dig depth (cm) ±SD | n | Mean feed time (s) ±SD | Mean dig depth (cm) ±SD | n |
| **Ground dig** | | | | | | |
| *A. custodiens* | 72 ± 50.7 | 4.5 ± 3.3 | 25 | 45 ± 34.6 | 3.6 ± 2.2 | 2741 |
| *M. natalensis* | 142 ± 251 | 5.7 ± 4.7 | 30 | 93 ± 80.7 | 6.7 ± 4.0 | 98 |
| *P. schistacea* | 99 ± 88.3 | 6.4 ± 4.6 | 23 | 57 ± 41.4 | 5.9 ± 3.1 | 46 |
| **Port feed** | | | | | | |
| *A. custodiens* | 0 | - | 0 | 27 ± 22.0 | - | 755 |
| *M. natalensis* | 86 ± 52.4 | - | 3 | 56 ± 35.9 | - | 52 |
| *P. schistacea* | 56 ± 50.7 | - | 4 | 29 ± 4.9 | - | 4 |
| **Totals** | | | | | | |
| *A. custodiens* | 72 ± 50.7 | | 25 | 41 ± 33.1 | | 3505 |
| *M. natalensis* | 137 ± 239. | | 33 | 80 ± 70.9 | | 154 |
| *P. schistacea* | 93 ± 85.2 | | 27 | 55 ± 40.4 | | 50 |

Zimbabwe where 51% of sightings were reported before 18h00. In the present study, however, only sub-adult pangolins appeared to be more active before 18h00 and could thus be considered more crepuscular. In contrast, adults were mainly nocturnal and were only occasionally active before 18h00 and only during winter (Fig. 4.1). It is likely that the pangolins in the above two studies were located at times when people were most active rather than pangolins, and these times probably coincided with the activity of predominantly sub-adult pangolins.

Sub-adult pangolins appear to forage within the same temperature range as adults (11°C - 25°C) and the length of their activity period is also similar to adults (Table 4.2), yet they prefer to forage during the late afternoon to early evening. In addition, they only forage within their natal ranges (pers. obs.) and therefore they do not appear to forage earlier to avoid competing with other pangolins for foraging sites. One reason for the sub-adults pronounced diurnal activity may be to avoid nocturnal predators such as lion. The scales of sub-adults are considerably weaker than that of adults and their body size is much smaller. This would make it easier for predators such as lion to damage the scales and pry them open. On several occasions very young pangolins of between three and five months old were observed leaving their mother in the den around midday to forage not more than 20 m from the den entrance (pers. obs.). The slightest sign of danger usually prompted them to scramble back to the safety of the den and their mother.

Thus it appears that very young pangolins are active earlier during the day and return to the den before their mother leaves to forage during the evening. As they grow older they venture out further and later until eventually as adults they switch from being predominantly diurnal to predominantly nocturnal. Although this appears to be their pattern of activity more data is needed to substantiate these findings.

The activity period of pangolins is governed by prey availability which is in turn determined mainly by temperature and photoperiod. Their prey, particularly *A. custodiens*, was less active at night and therefore more densely aggregated within the underground galleries. Steyn (1954) noted that the activity of *A. custodiens* decreased significantly at low temperatures and low light intensities. Thus pangolins forage mainly nocturnally within a preferred temperature range of between 11 and 25°C when their prey is available near the soil surface. One example of how activity period is governed by prey activity is manifested in numbats *Myrmecobius fasciatus*. They are fully diurnal marsupials because of their dependence on termite prey which are more active in their foraging galleries by day than by night (Calaby 1960; Friend 1982).

Seasonal variation in activity period is often also determined by prey activity. Aardwolves change from being nocturnal and feeding almost exclusively on the termite species *Trinervitermes trinervoides* during summer to being crepuscular and feeding on both *T. trinervoides* and *H. mossambicus* during winter (Richardson 1987a, 1987b). Although pangolins are not as specialised as aardwolves in their feeding habits, the seasonal variation in their activity period was also influenced by prey availability. Ant activity was reduced by cold temperature and pangolins foraged earlier during winter when temperatures were warmer and ants more accessible. Thus temperature was an important factor in determining the pangolin's activity during winter; particularly the time they became active. In contrast, summer temperatures rarely fell below 15°C (within the pangolins preferred temperature range) and was thus not significant in determining their activity. Humidity on the other hand appeared to be more important in determining pangolin activity than temperature during summer. A study of ants in the Letaba district of the Eastern Transvaal revealed that there was a significant negative correlation between the activity of *A. custodiens* and humidity (Steyn 1954). Thus as humidity increased the activity of *A. custodiens* decreased and they became more available as prey. Although humidity may have had some influence on the pangolin's activity during summer, the prey availability appeared paramount.

Interestingly, the average length of the pangolin's activity period was similar during summer and winter and was governed mainly by the amount of prey they were able to locate. This is probably why the correlation between the time that pangolins returned to their dens and the temperature was not significant. The importance of prey availability in determining the time that pangolins were active is clearly illustrated in Fig. 4.4 which shows that they were generally active for shorter periods during the months when their feeding intensity was higher, and visa versa.

The time that pangolins became active largely determined the time they returned to their dens. Thus when they became active early they usually returned to their dens relatively early and visa versa. During summer, however, their activity appeared less predictable than during winter even though they generally became active later when temperatures were slightly cooler. This suggests that the overall prey availability may be more consistent during winter than during summer. During winter the ants were usually inactive and thus more available to pangolins, whereas during summer the ant activity was considerably higher and more erratic, particularly after rains, resulting in a more inconsistent availability of prey. When the ants were more active they were less available underground and were thus preyed on less frequently. For example, the overall frequency of feedings by pangolins was at its lowest during February and March 1994 when the activity of *A. custodiens* was the highest (Fig. 4.10).

## Diet

Kingdon (1971) rated pangolins as selective feeders of ants and termites, and the present study verified their selectivity for certain prey species. Firstly, the number of prey species available during the study period did not appear to determine the number of species that was preyed on by pangolins (Fig. 4.8). Secondly, they preyed predominantly on species larger than 0.5 cm and thirdly only six species accounted for as much as 97.7% of the overall diet of which *A. custodiens* made up 77%. Thus only 11% (six out of 54 species) constituted this large proportion of their diet. It appears that pangolins were not necessarily preying on the most abundant species since three species (all smaller than 0.5 cm) were more abundant than *A. custodiens* (see Table 3.2) yet only accounted for 0.8% of their diet. Moreover, five of the six predominant species in the pangolin's diet were low in abundance (cf. Fig. 4.9 and Table 3.1).

This selectivity for such a high proportion of *A. custodiens* is largely due to its availability as prey to pangolins. Redford (1984, 1987) suggested that myrmecophagous mammals probably prey on the most available species rather than attempt to select species with higher nutritional value. A distinction must be drawn between prey abundance and prey availability since the most abundant species is not necessarily the most available.

Ant and termite availability to pangolins is determined by two prominent factors. Firstly, the nesting behaviour of ants and termites, in particular their depth below the soil surface, is probably the major factor determining their availability. The morphological adaptation that pangolins share with some of the other typical myrmecophagous mammals is strong forelimbs with hard claws modified for digging. However, they are not as well adapted for digging deep into hard soil as the aardvark *Orycteropus afer* (Melton 1976), the giant armadillo *Priodontes maximus* (Redford 1985b) and the giant pangolin *Manis gigantea* (Kingdon

1984). Thus several common termite species especially of the genus *Macrotermes* were not available to pangolins since their nests are constructed with a hard outer crust of compacted soil (Skaife 1979) making the nest galleries impenetrable to pangolins. On the other hand, the predominant species in the pangolins diet *A. custodiens* store's grass seeds and honeydew in a mass of horizontal channels and galleries 4 - 7 cm below the soil surface (Bond & Slingsby 1983). Thus, when pangolins preyed on this species, they were only required to dig shallow digs with the result that their foraging efficiency was probably greatest while their digging effort was just sufficient to expose the relatively dense aggregations of ants within the active galleries.

Secondly, the activity period of ants and termites and their foraging activity within the underground galleries also largely determines whether they are available as prey. The harvester termite *H. mossambicus* nests approximately 1.5 m below the soil surface (Hartwig 1965) which is inaccessible to pangolins, thus they were preyed on only when they were active in secondary aggregations in the nest ports at the soil surface.

Although *A. custodiens* predominated in the pangolins diet throughout the study period, it was preyed on less during summer than winter (Fig. 4.9). This was mainly due to the large increase of *M. natalensis* in their diet during the summer months (Fig. 4.9) and appeared to be related to the higher rainfall during summer. The highest rainfall figures of 147 mm and 70 mm were recorded during December 1993 and March 1994 respectively and these were also the months when *M. natalensis* constituted a large proportion of the pangolin's diet (35% and 32% respectively).

The harvester termite *H. mossambicus* was the only termite species that made a perceptible contribution to the pangolin's diet and was preyed on almost exclusively during the dry season (May to September). Bat-eared foxes *Otocyon megalotis* in the Kalahari (Nel 1978) and white-tailed mongooses *Ichneumia albicauda* on the Serengeti plains (Waser 1980) also preyed on *H. mossambicus* predominantly during the dry seasons. Harvester termites usually collect dry grass since green grass is apparently toxic to certain species (Sands 1961; Botha & Hewitt 1978; Ohiagu 1979). Thus, harvesters such as *H. mossambicus* are more active during the dry season when more dry grass is available. This has been recorded for *H. mossambicus* in Southern Africa (Nel & Hewitt 1969) and was also observed during the present study.

### Foraging behaviour

The foraging behaviour of pangolins is unique in the sense that they have distinctive foraging patterns. In general they locate their prey by following a haphazard zigzag path that probably enables them to cover a larger area within feeding sites. This zigzagging behaviour was also observed in the aardvark (Melton 1976) and it apparently enabled them to inspect a strip of about 30 m wide while searching for prey. It appears that pangolins are very familiar with the area in which they forage and know the location of many of their feeding sites. This was confirmed by the directional path that they often followed when walking between feeding sites and dens (pers. obs.). The circular foraging pattern manifested by pangolins (Fig. 4.12c) is particularly interesting in this regard since it appears that they have a strategy whereby a designated route is followed through a number of chosen feeding sites. These feeding sites may have yielded a high density of prey species in the past since the same route may have been followed previously with a relatively high degree of foraging success. There were several occasions when pangolins were observed returning to the same feeding site several weeks and even several months later (pers. obs.).

The duration and depth of feeding bouts, the number of feedings and the distances between feedings within feeding sites varied considerably and was determined by two major factors; prey availability and prey value. Thus, the foraging success of pangolins was largely dependent on these two factors. According to Sih (1980) a predator that takes two or more bites to consume an entire prey item faces a decrease in the prey value after each bite. Similarly, from the time that a myrmecophagous predator begins feeding on an ant or termite colony it experiences a decrease in the prey value as a result of the rapid response of the ants and termites following predator attack (Redford 1985a). This decrease in prey value is caused by colony defence mechanisms exhibited by the different prey species that in turn limit predation and result in short duration feeding bouts typical of mammalian myrmecophages (Redford 1985a, 1987). This suggestion is supported by the present study since the average duration of pangolin feedings were only 40 sec and the majority of feedings were shorter than one minute.

The prominent prey species of pangolins, *A. custodiens,* are very aggressive ants that swarm and bite fiercely following predator attack, and like other members of the Formicinae they also spray formic acid from a poison gland or inject it into the bite wounds (Skaife 1979). *Azteca* ants are apparently effective in repelling *Tamandua* anteaters by swarming over them in large numbers, biting, and secreting chemicals that may act as repellents (Lubin *et al.* 1977; Lubin & Montgomery 1981). The soldiers of the termite species *H. mossambicus* have powerful mandibles that function solely to defend the colony against predator attack (Wilson & Clarke 1977). These soldiers are effective in deterring pangolins since the duration of feeding bouts were very short (usually < 10 sec) and pangolins displayed considerable discomfort when preying on this species (Swart 1992; pers. obs.). Very short duration feedings (ca. eight sec) on *H. mossambicus* were also recorded for bat-eared foxes *Otocyon megalotis* in the Kalahari (Nel 1978).

Although this aggressive behaviour probably reduces predation, an equally important factor responsible for reducing the prey value to pangolins appears to be the mobility of the different prey species. *A. custodiens,* for example, are fast moving ants that disperse quickly while swarming (pers. obs.) thus reducing the density in their underground galleries soon after being attacked. On the other hand the species *M. natalensis* and *P. schistacea* are relatively slow moving (pers. obs.) and not as aggressive as *A. custodiens* with the result that higher densities are maintained for longer within their underground galleries following predator attack. Thus, the feeding durations are considerably longer when pangolins preyed on these two species (Table 4.3). Foraging efficiency is therefore largely governed by the prey value and since each species differs in prey value, the duration of feeding bouts on each species probably varies according to an optimal level of food intake.

Pangolins appeared to forage mainly from secondary aggregations of ants or termites since the digs were very shallow and a high proportion of feeding bouts (28%) was directly from an active ant or termite port. Interestingly, the average duration of feedings from the active ports of the various species was significantly shorter than from digs. A reasonable explanation for this is probably that while ants or termites are active in and out of the port their density is expected to be lower than when they are relatively inactive within the underground galleries. Thus, although the prey value from an active port is lower than from the ground digs, less energy is required to extract prey from the ports. On the other hand, if only a little additional energy was required to expose the underground galleries where higher densities of prey can be found then it would be more beneficial for pangolins to feed from these digs. This appears to be the strategy adopted by pangolins since the majority of feedings (71%) were from ground digs, with an average dig time of only 8.7 sec and an average dig depth of only 3.8 cm per feeding bout.

Interestingly, the feeding durations were dependent on the depth that the various prey species were located below the soil surface. Pangolins therefore preyed longer on species that were located deeper underground, suggesting that species that were located at greater depths may be higher in prey value. This is clearly illustrated by the highly significant regression in Fig. 4.16. It is likely that pangolins dig deeper for species that have a higher prey value because these species can be preyed on for longer during each feeding bout. For example, *M. natalensis* and *P. schistacea* can be considered high in prey value since they are both sluggish ants and have a relatively poor defence against predation by pangolins (pers. obs). Thus, it appears beneficial for pangolins to dig deeper to the high density areas of the nests when preying on these species. In contrast, *H. mossambicus* are considerably lower in prey value since the fierce snapping mandibles of their soldiers are efficient in deterring pangolins and are thus preyed on for very short durations close to the soil surface. Moreover, the high density areas of their nests are deep below the soil surface (ca. 1.5 m) and pangolins would need to put a large effort into digging for a very low reward. On the other hand, *A. custodiens* can be considered an optimum prey species since they have extensive nests with relatively dense secondary aggregations of ants close to the soil surface (Steyn 1954; Bond & Slingsby 1983). In addition, they are abundant and appear to have a moderate prey value since they were frequently preyed on and the feeding durations were relatively long.

There was a considerable seasonal variation in the depth that pangolins excavated in the soil to extract their prey. During the summer, when the soil was softened by the rainfall, pangolins were able to dig deeper into the higher density areas of the nests where the prey value was higher. The data supported this since the average duration of the feedings was longer during summer than during winter. Digging deeper also enabled them to prey more frequently on species that were located deeper underground. This is probably one of the reasons why *M.*

*natalensis* increased in the pangolins diet from 2% during winter to 16% during summer. This ability to dig deeper during summer may also allow pangolins to compensate for the lower prey value of *A. custodiens* during summer. This species was preyed on less during summer as a result of their higher activity above ground and thus lower densities within their underground galleries. Thus, although pangolins foraged with similar feeding intensity (feed time per hour) during summer and winter, the average distance between feedings was greater and the frequency of feedings lower during summer. This meant that pangolins had to locate and dig into the higher density areas of the ant and termite nests during summer to compensate for the lower availability of prey. Digging was probably made easier by the softer soil and since the higher density areas of nests could be reached the prey value per feeding bout increased with the result that the duration of feeding bouts was longer.

The positive correlation between feeding duration and the dig depth may also be an interpretation of how efficiently pangolins were at extracting their prey from below the soil surface. If a higher prey value is associated with deeper digs then pangolins are expected to feed for longer when they dig deeper and for shorter durations when digs are shallower. In addition, only the more experienced pangolins such as adults with a better knowledge of their food source would be expected to use this strategy. The more significant the correlation the more efficiently prey is extracted. The correlation between the mean feed time and the mean dig depth was significant for all adult pangolins, yet not for the sub-adult pangolin "Imini" (Table 4.5). Thus the sub-adult pangolin appeared less efficient at extracting prey from below the soil surface.

Although all adult pangolins appeared efficient at extracting prey, there were individual differences in their feeding behaviour. According to Redford (1987) individual differences in feeding may be non-resource related. For example, the maternal care of many myrmecophagous mammals may enable "cultural" transmission of food preferences that could account for such individual differences (McGrew 1983). This form of care, which involves the mother carrying the infant with her while she is out foraging, was observed in three genera of anteaters (Redford 1987). According to Redford (1987) the young may learn the same prey preferences and foraging locations from the mother while accompanying her while she feeds and eventually feeding with her. Sub-adult pangolins, however, were never observed foraging with their mothers and the only time they were carried by their mothers was when they were being moved from one den to another. When a sub-adult was being moved, the mother walked straight to the new den without stopping to feed. Thus, although extracting prey efficiently appears to be a learned behaviour for sub-adult pangolins it is probably achieved by trial and error. This may be an explanation for the low feeding efficiency recorded for the sub-adult pangolin "Imini".

Ant and termite alates and their larval and pupal stages are apparently higher in nutritional value and have a substantially higher fat content than other castes (Redford 1984). Thus, when these castes are available they should be selected in preference to other castes because of their higher prey value. According to Redford (1987) alates within a nest can change the food value of an ant or termite colony. This was also observed for echidnas (Griffiths & Simpson 1966) and *Tamandua* anteaters (Lubin & Montgomery 1981), since in both cases the presence of alates or prealates in a nest was highly correlated with longer feeding bouts on the nest. Pangolins never preyed on ant or termite alates, however, when they preyed on the ELP stages of ants the average duration of feeding bouts was also significantly longer.

Kingdon (1971) recorded *M. temminckii* in East Africa preying predominantly on the juvenile stages of *Crematogaster, Odontotermes* and *Microcerotermes.*

However, in the present study these juvenile stages (eggs, larvae and pupae) did not make a significant contribution to their diet since they were recorded in only 1.9% of the total feeding bouts. In addition, they were preyed on almost exclusively during summer and only when they were available. Steyn (1954) recorded very few ELP stages in the nests of *A. custodiens* during winter and a peak egg production during August and January. The availability of the ELP stages to pangolins probably also depended on their depth below the soil surface during the different seasons. The ELP stages of *A. custodiens* are usually situated in several queen cells between 10 and 50 cm below the soil surface (see Steyn 1954). This species and several others in the Formicidae apparently move their brood closer to, or further away from the soil surface as the temperature changes, so that an optimal temperature for the development of the brood is maintained (pers. com. H.G. Robertson, S.A. Museum, P.O. Box 61, Cape Town, 8000). Thus, the ELP stages of *A. custodiens* were probably unavailable to pangolins for much of their foraging time, and this may be the main reason why only 0.7% of their total feeding bouts were on the ELP stages of this species.

# CHAPTER 5

# FORAGING HABITAT SELECTION OF PANGOLINS

## INTRODUCTION

Previous studies have indicated the types of habitat where *M. temminckii* were found (see Kingdon 1971; Smithers 1983), but none have described their selection for habitat types preferred as foraging areas. Thus, this study is the first to examine the habitat selection and utilisation by *M. temminckii*.

This chapter describes the overall habitat selectivity as well as the seasonal variation of habitat selection by *M. temminckii*. The difference in the extent of habitat selection between the different study animals is also compared and the contribution of the various prey species to the pangolin's diet within each habitat type is examined. This information is expected to provide important clues for determining the habitat requirements of *M. temminckii* in this region.

## METHODS

Nine habitat types' representative of the study area were identified and listed in Table 5.1. Habitat types were recorded concurrently with feeding records (see methods in Chapter 4) so that the number of feeding bouts recorded in each habitat type could be used to determine the degree of habitat selectivity by foraging pangolins. The key species of trees, shrubs and grasses used to identify the various habitat types are outlined in Chapter 2.

The soil type that pangolins foraged on was also recorded with each feeding bout. The soils of the study area occur in distinctive catenary sequences on

**Table 5.1.** Relative availability data for habitat types in the study area (Funston 1992).

| Habitat | Total area (ha) | Relative area |
|---|---|---|
| Marula/Combretum sand savanna (MC) | 7123 | 0.42 |
| Grassland savanna clearings (GC) | 2217 | 0.13 |
| Mixed tree savanna (MT) | 2327 | 0.14 |
| Calc brack thicket (CB) | 558 | 0.03 |
| Riverine thicket (RT) | 1455 | 0.09 |
| Knobthorn black turf savanna | 1043 | 0.06 |
| Knobthorn red turf savanna | 1468 | 0.09 |
| Riverine floodplain | 143 | 0.01 |
| Turf grassland | 468 | 0.03 |
| Rocky outcrop | 149 | 0.01 |
| Total | 16951 | 1.00 |

granitoid rocks and were therefore grouped according to these sequences and classified as follows: a) **deep sands (DS)** of the crests including moderately deep to deep apedal eutrophic coarse sands; b) **hydromorphic soils (HC)** of the upper slopes including shallow to moderately deep grey hydromorphic sands and clays; c) **duplex soils (DX)** of footslopes made up of coarse apedal sand on prismatic structure clay; and d) **alluvial soils (AL)** of the valley bottoms including alluvial sandy clay loams.

The Marula/*Combretum* sand savanna (MC) and riverine thicket (RT) habitats are situated on the crests and valley bottoms respectively, whereas the grassland savanna clearings (GC), mixed tree savanna (MT) and calc brack thicket (CB) habitats are usually situated on the slopes.

The chi-square test was used to determine whether there was a significant difference between the expected utilisation of habitat types (based on their availability) and the observed frequency that they were foraged in. However, if a statistically significant difference is found between the utilisation and availability of the habitat types, the chi-square test is not able to determine which habitat types' pangolins preferred to forage in. Thus, the data was further investigated by using Bonferroni confidence intervals (Neu, Byers & Peek 1974; Byers, Steinhorst & Krausman 1984) to determine which habitat types were being preferred.

Overall selectivity was quantified using the index $S$ (McNaughton 1978), where

$$S_{\mathrm{j}} = \Sigma \mid P_{\mathrm{H_i}} - P_{\mathrm{F_i}} \mid /2$$

and $P_{\mathrm{H_i}}$ = proportional abundance of the $i$-th habitat in the study area, and $P_{\mathrm{F_i}}$ = proportional abundance of feeding bouts in the $i$-th habitat selected by pangolin j. A zero value denotes no selectivity, whereas a score of one represents maximum selectivity.

## RESULTS

### Habitat selectivity and utilisation, and the catenary sequence

The habitat selectivity of 11 pangolins was studied between June 1993 and July 1994 and all study animals exhibited a relatively high degree of habitat selectivity (Table 5.2). Of these 11 study animals, five revealed increased selectivity during summer, although this was only marked for the female "Ozela", and three increased their selectivity during winter. The data was incomplete for the remaining three individuals since they were observed for only one of the two seasons. Although there were individual differences among pangolins, there was no significant difference between summer and winter in their overall habitat selectivity ($t = 0.311$; df = 17; $P > 0.7$).

Details of habitat type selection are given in Tables 5.3 and 5.4. If the value for the expected proportion of feeding bouts $P_i$ falls within the Bonferroni confidence interval, then the null hypothesis is accepted and there was no significant difference between the proportion of feeding bouts and the proportion of available habitat. Conversely, if $P_i$ is greater than the confidence interval then the null hypothesis is rejected and the habitat was utilised significantly less than expected. Similarly, a $P_i$ value smaller than the confidence interval indicates that the habitat was utilised significantly more than expected.

Pangolins selected against feeding in the marula/*Combretum* and riverine thicket habitats during both winter and summer months ($P < 0.001$), and the overall proportion of feeding bouts recorded in these habitats was only 7.3% and 0.9% respectively. During both winter and summer the grassland, mixed tree and calc brack habitat types were selected in preference to the other habitat types and the observed proportion of feeding bouts in these habitat types was significantly higher than the expected proportions ($P < 0.001$; Table 5.3 and Table 5.4). In

**Table5.2.** The habitat selectivity shown by 11 pangolins in the study area.

| Animal | Habitat selectivity index (*S*) Winter | Habitat selectivity index (*S*) Summer |
|---|---|---|
| Azana | 0.863 | - |
| Imini | 0.692 | 0.836 |
| Jobu | 0.683 | 0.615 |
| Lola | - | 0.863 |
| Nina | 0.663 | 0.675 |
| Ozela | 0.415 | 0.828 |
| Penula | 0.869 | 0.436 |
| Shumi | 0.534 | 0.697 |
| Vunga | 0.449 | 0.569 |
| Yela | 0.750 | 0.613 |
| Zinga | 0.683 | - |
| Total selectivity (*S*) | 0.618 | 0.609 |

**Table 5.3.** The Chi-square statistics and simultaneous Bonferroni confidence intervals for the utilisation of habitat types by nine pangolins during winter ($\chi^2 = 6207$; df = 5; $p < 0.001$; null hypothesis rejected). The confidence intervals were determined at the 99% level.

| Habitat | Observed No. of feeding bouts | Expected No. of feeding bouts | Chi-square values | Observed proportion of bouts $P_{io}$ | Expected proportion of bouts $P_i$ | Bonferroni intervals for $P_i$ |
|---|---|---|---|---|---|---|
| MC | 194 | 1057 | 704 | 0.077 | 0.422 | $0.057 < P < 0.097$ |
| GC | 829 | 328 | 763 | 0.331 | 0.131 | $0.295 < P < 0.366$ |
| MT | 874 | 344 | 815 | 0.349 | 0.137 | $0.313 < P < 0.384$ |
| CB | 601 | 83 | 3247 | 0.240 | 0.033 | $0.208 < P < 0.272$ |
| RT | 9 | 216 | 198 | 0.004 | 0.086 | $-0.001 < P < 0.008$ |
| OTH | 0 | 479 | 479 | 0.000 | 0.191 | |
| Totals | 2507 | 2507 | 6207 | 1.000 | 1.000 | |

OTH = the other habitats combined (see Table 5.1)

**Table 5.4.** The Chi-square statistics and simultaneous Bonferroni confidence intervals for the utilisation of habitat types by eight pangolins during summer ($\chi^2 = 5097$; df = 5; $p < 0.001$; null hypothesis rejected). The confidence intervals were determined at the 99% level.

| Habitat | Observed No. of feeding bouts | Expected No. of feeding bouts | Chi-square values | Observed proportion of bouts $P_{io}$ | Expected proportion of bouts $P_i$ | Bonferroni intervals for $P_i$ |
|---|---|---|---|---|---|---|
| MC | 166 | 934 | 631 | 0.075 | 0.422 | $0.054 < P < 0.096$ |
| GC | 485 | 290 | 131 | 0.219 | 0.131 | $0.186 < P < 0.252$ |
| MT | 1115 | 304 | 2162 | 0.503 | 0.137 | $0.463 < P < 0.543$ |
| CB | 417 | 73 | 1618 | 0.188 | 0.033 | $0.157 < P < 0.220$ |
| RT | 32 | 191 | 132 | 0.014 | 0.086 | $0.005 < P < 0.024$ |
| OTH | 0 | 423 | 423 | 0.000 | 0.191 | |
| Total | 2215 | 2215 | 5097 | 1.000 | 1.000 | |

addition, pangolins foraged in similar proportions in these three habitat types during winter, thus there was no significant difference in the number of feeding bouts ($F_{2,15} = 0.39$; $P = 0.7$). In contrast, a significant difference in the number of feeding bouts was recorded between the above three habitat types during summer ($F_{2,21} = 4.36$; $P < 0.03$), with the majority (55%) occurring in the mixed tree habitat type (Table 5.4). The observed proportion of feeding bouts in the mixed tree, calc brack and grassland habitat types was also significantly higher than the expected proportion during summer ($P < 0.001$).

The above seasonal variation in the habitat utilisation of pangolins is illustrated in Fig. 5.1(a). This illustration also closely reflects the proportion of feeding bouts recorded in each habitat type when pangolins preyed on *A. custodiens*, since this species accounted for approximately 77% of their diet. The seasonal variation in habitat utilisation while pangolins preyed on *A. custodiens* is depicted in Fig. 5.1(b). During the winter and early summer months of June to October 1993 a larger proportion of feedings was recorded in the calc brack and grassland habitat types than the mixed tree habitat, whereas during mid-summer the proportion of feedings increased in the mixed tree habitat type and decreased in the grassland and calc brack habitat types (Fig. 5.1a). The proportion of feedings also increased in the marula/*Combretum* habitat type during the late summer and early winter of 1994 but then decreased towards mid-winter.

Interestingly, the calc brack habitat type was included in the foraging ranges of only three pangolins, namely: Jobu, Nina and Yela, and although this habitat type was represented by a mere 3% of the study area (see Table 5.1), 42% of the feeding bouts recorded on these three pangolins were in the calc brack habitat type. The high chi-square value of 3247 is evidence of the significantly high habitat selection for the calc brack habitat type during winter (Table 5.3).

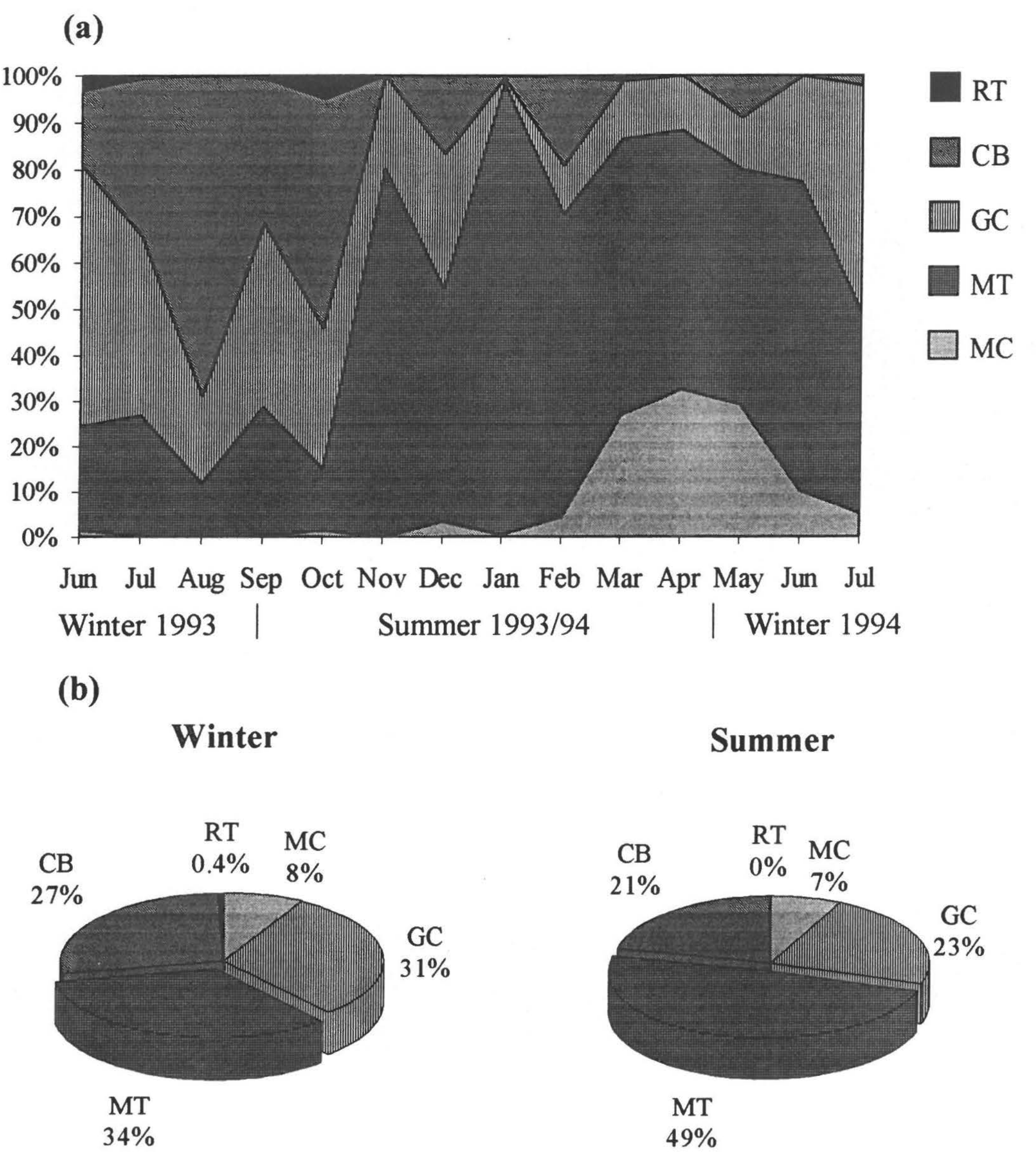


**Fig. 5.1.** The seasonal variation in the proportion of feeding bouts recorded on all species (a) and on the ant species *A. custodiens* (b) in the five different habitat types utilised by pangolins.

The above habitat types are associated with a catenary sequence of soil complexes from hill crest to valley bottom (Fig. 5.2). Pangolins foraged predominantly on structured soils of the slopes between the crests and valley bottoms where the compacted clay soils of the footslopes appeared most favourable. Of the total feeding bouts recorded 87.5% were on the slopes of the hills, whereas only 10.4% and 2.1% were recorded on the crests and valley bottoms respectively.

There was also a considerable seasonal variation in the proportion of feeding bouts recorded in the various regions of the catenary sequence. During the winter months feeding bouts were distributed evenly between the upper slopes and footslopes, whereas during summer a larger proportion was recorded on the footslopes (Fig. 5.2). The proportion of feedings on the crests was also higher during the summer months compared to winter (Fig. 5.2).

The relationship between the duration of feeding bouts and the depth of the feeding digs discussed in Chapter 4 is also manifested on the various soil types of the catenary sequence. That is, the mean feeding bout was longer and the mean dig depth deeper in the deep sands (DS) and the alluvial (AL) soils of the crests and valley bottoms, whereas shorter feeding bouts and shallower digs were recorded in the hydromorphic (HY) and duplex (DX) soils of the slopes (Fig. 5.3). The correlation between the mean duration of feeding bouts and the mean dig depth recorded on these four major soil types is significant ($r = 0.97$; $df = 2$; $P < 0.05$).

### Feeding strategy and diet in relation to habitat utilisation

Over and above the pangolins' selection for particular foraging areas, their feeding strategy also varied according to the habitat and soil type where they foraged. There was a significant difference in the overall mean duration of

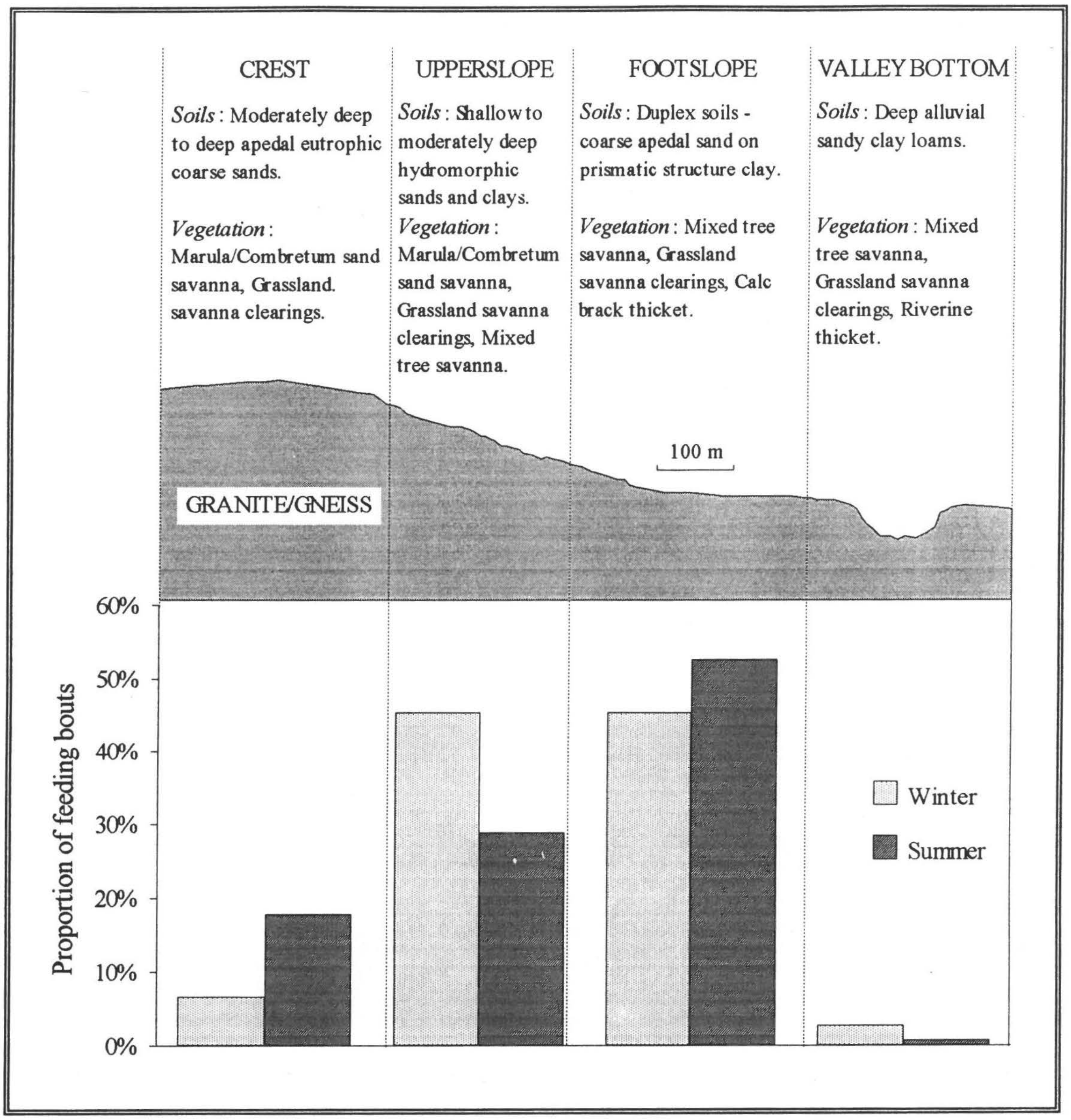


**Fig. 5.2.** A typical catenary sequence from crest to valley bottom, depicting the seasonal difference in the proportion of feeding time observed in each region. The most common soil and vegetation types are also included for each region on the catenary sequence.

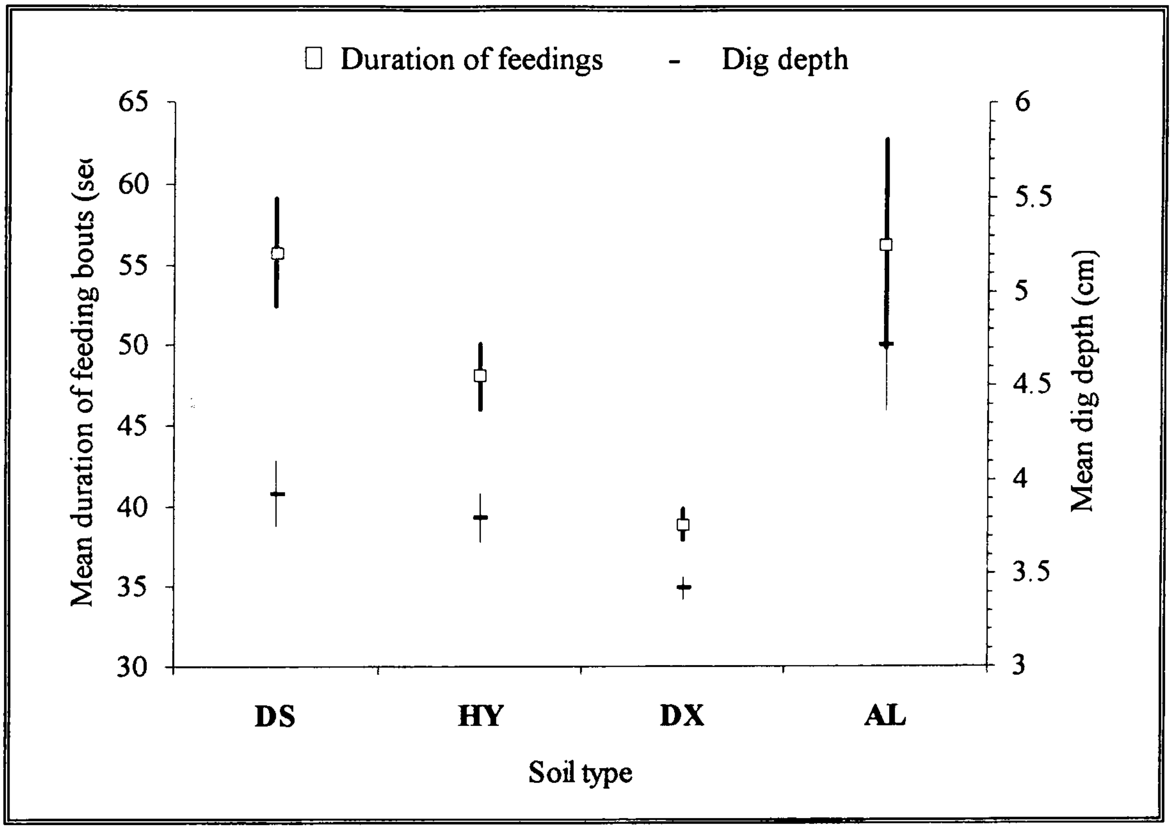


**Fig. 5.3.** The relationship between the duration of feeding bouts and the depth of diggings on the four major soil types in the study area. Vertical lines represent one Standard Error. **DS** = deep sands, **HC** = hydromorphic soils, **DX** = duplex soils and **AL** = alluvial soils.

feeding bouts recorded in each habitat type ($F_{4,4668} = 16.9$; $P < 0.001$). The longest duration of 48 sec (SD = 39 sec) was recorded in the riverine thicket habitat type, whereas the shortest duration of 30 sec (SD = 25 sec) was recorded in the calc brack habitat type. The overall mean duration of feeding bouts recorded in the remaining three habitats, namely: the mixed tree, grassland and marula/*Combretum* habitat types, were 43 sec (SD = 53 sec), 41 sec (SD = 39 sec) and 44 sec (SD = 34 sec) respectively. Similarly, the overall mean depth of the feeding digs was also the greatest in the riverine thicket habitat (4.7 cm; SD = 2.3 cm) and smallest in the calc brack habitat (3.2 cm; SD = 1.8 cm) with the mean depth of the digs being significantly different in each habitat type ($F_{4,3303} = 19.88$; $P < 0.001$). An overall mean dig depth of 4.0 cm (SD = 2.8 cm) was recorded in the mixed tree habitat type, 3.6 cm (SD = 2.0 cm) in the grassland habitat and 4.2 cm (SD = 2.7 cm) in the marula/*Combretum* habitat type.

The seasonal variation in the duration of feeding bouts and the depth of feeding digs for each habitat type is given in Table 5.5 and 5.6 respectively. Although the overall mean duration of feeding bouts was longer during summer than during winter (see Chapter 4), this difference was significant only in the mixed tree habitat type ($t = 3.51$; df = 1987; $P < 0.001$). Although the mean duration of feeding bouts recorded in the riverine thicket habitat type appears significantly longer during summer compared to winter, this is not conclusive since only nine feeding bouts were recorded in this habitat during winter (Table 5.5). The overall mean depth of the feeding digs was also deeper during summer months than winter months (see Chapter 4), but this difference was only significant in the mixed tree habitat type ($t = 4.43$; df = 1372; $P < 0.001$) and the marula/*Combretum* habitat type ($t = 4.07$; df = 278; $P < 0.001$). As mentioned above only nine feeding bouts were recorded in the riverine thicket habitat, thus

**Table 5.5.** Seasonal differences in the duration of feeding bouts recorded in each habitat type.

| Habitat type | Summer (Sep 93 - Apr 94) Total No. of feeding bouts | Summer (Sep 93 - Apr 94) Total feeding time (min) | Summer (Sep 93 - Apr 94) Mean feed time per bout (sec) ±SD | Winter (Jun - Aug 93 & May - Jul 94) Total No. of feeding bouts | Winter (Jun - Aug 93 & May - Jul 94) Total feeding time (min) | Winter (Jun - Aug 93 & May - Jul 94) Mean feed time per bout (sec) ±SD |
|---|---|---|---|---|---|---|
| MT | 1115 | 870 | 47 ±61 | 874 | 560 | 38 ± 39 |
| GC | 485 | 319 | 40 ±39 | 829 | 588 | 43 ± 39 |
| MC | 166 | 128 | 46 ±36 | 194 | 138 | 43 ± 32 |
| CB | 417 | 215 | 31 ±27 | 601 | 298 | 30 ± 23 |
| RT | 32 | 28 | 53 ±43 | 9 | 5 | 34 ± 19 |
| Totals | 2216 | 1563 | 42 ±50 | 2507 | 1589 | 38 ± 35 |

**Table 5.6.** Seasonal differences in the depth of feeding digs recorded in each habitat type.

| | Summer (Sep 93 - Apr 94) | | | Winter (Jun - Aug 93 & May - Jul 94) | | |
|---|---|---|---|---|---|---|
| Habitat type | Total No. of feeding bouts | Total ground digs | Mean dig depth (cm) ±SD | Total No. of feeding bouts | Total ground digs | Mean dig depth (cm) ±SD |
| MT | 1115 | 812 | 4.3 ±3.1 | 874 | 562 | 3.7 ± 2.2 |
| GC | 485 | 331 | 3.4 ±2.2 | 829 | 585 | 3.6 ± 1.9 |
| MC | 166 | 126 | 4.8 ±3.1 | 194 | 154 | 3.6 ± 2.3 |
| CB | 417 | 297 | 3.3 ±2.2 | 601 | 440 | 31. ± 1.5 |
| RT | 32 | 28 | 5.1 ±2.5 | 9 | 9 | 4.1 ± 1.6 |
| Totals | 2216 | 1595 | 4.0 ±2.8 | 2507 | 1750 | 3.5 ± 2.0 |

although the mean dig depth was deeper in this habitat more data are required to validate this result.

There is a considerable variation in the number of species preyed on by pangolins in the various habitat types. Of the total 20 species of ants and termites preyed on, 18 species were preyed on in the mixed tree habitat type, 16 species in the grassland habitat type, nine species each in the marula/*Combretum* and calc brack habitat types, and eight species in the riverine thicket habitat type. Thus, approximately twice as many species were preyed on in the grassland and mixed tree habitat types compared to the remaining three habitat types. More species were preyed on during winter than summer in all habitat types (Fig. 5.4).

Pangolins preyed on the various species of ants and termites at different intensities in the various habitat types. The pangolins (n = 11) overall feeding intensity for all habitats combined was 577 seconds per hour. Their feeding intensity was highest in the calc brack habitat (728 seconds per hour), followed by the grassland habitat (714 seconds per hour), the mixed tree habitat (593 seconds per hour) and the marula/*Combretum* habitat (280 seconds per hour), while the lowest value of 233 seconds per hour was recorded in the riverine thicket habitat. These feeding intensities differed significantly between habitat types ($F_{4,61} = 29.76$; $P < 0.001$).

The seasonal variation of the pangolins feeding intensity in each habitat type is illustrated in Fig. 5.5 and the seasonal variation of their feeding intensity on each species in each habitat is listed in Table 5.7. The pangolin's feeding intensity on the species *A. custodiens* was higher than on all other species combined during summer and winter and in all habitat types except the riverine thicket habitat type (Fig. 5.6; Table 5.7). In the riverine thicket habitat their feeding intensity

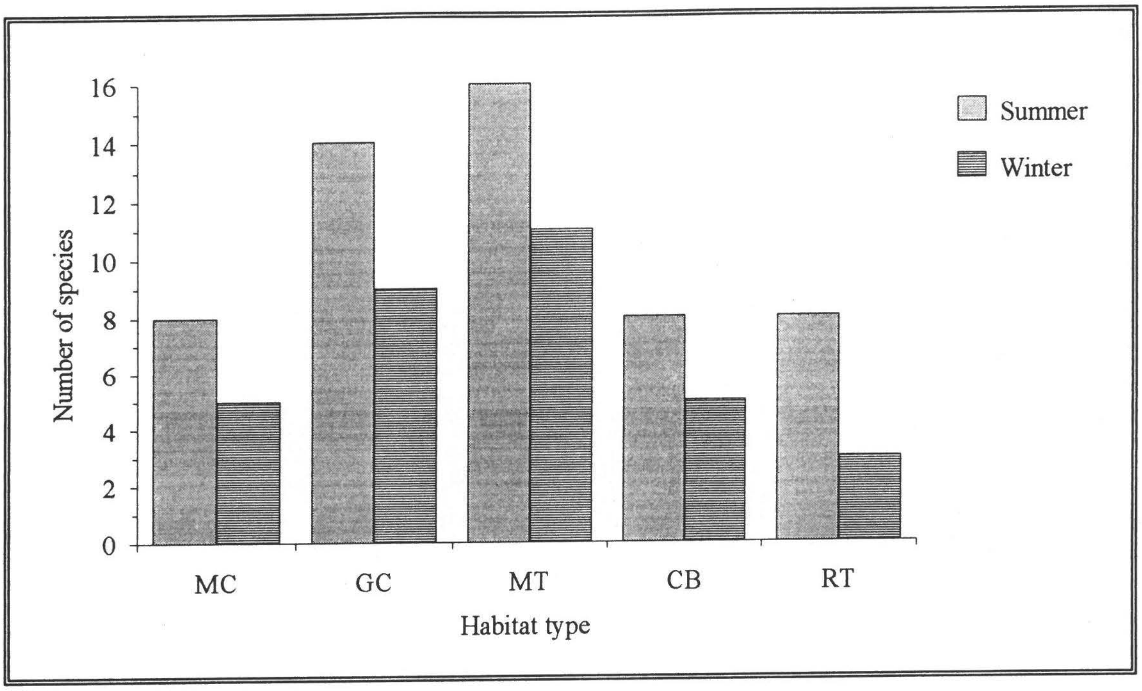


**Fig. 5.4** The seasonal variation in the number of species preyed on by pangolins in the five different habitat types.

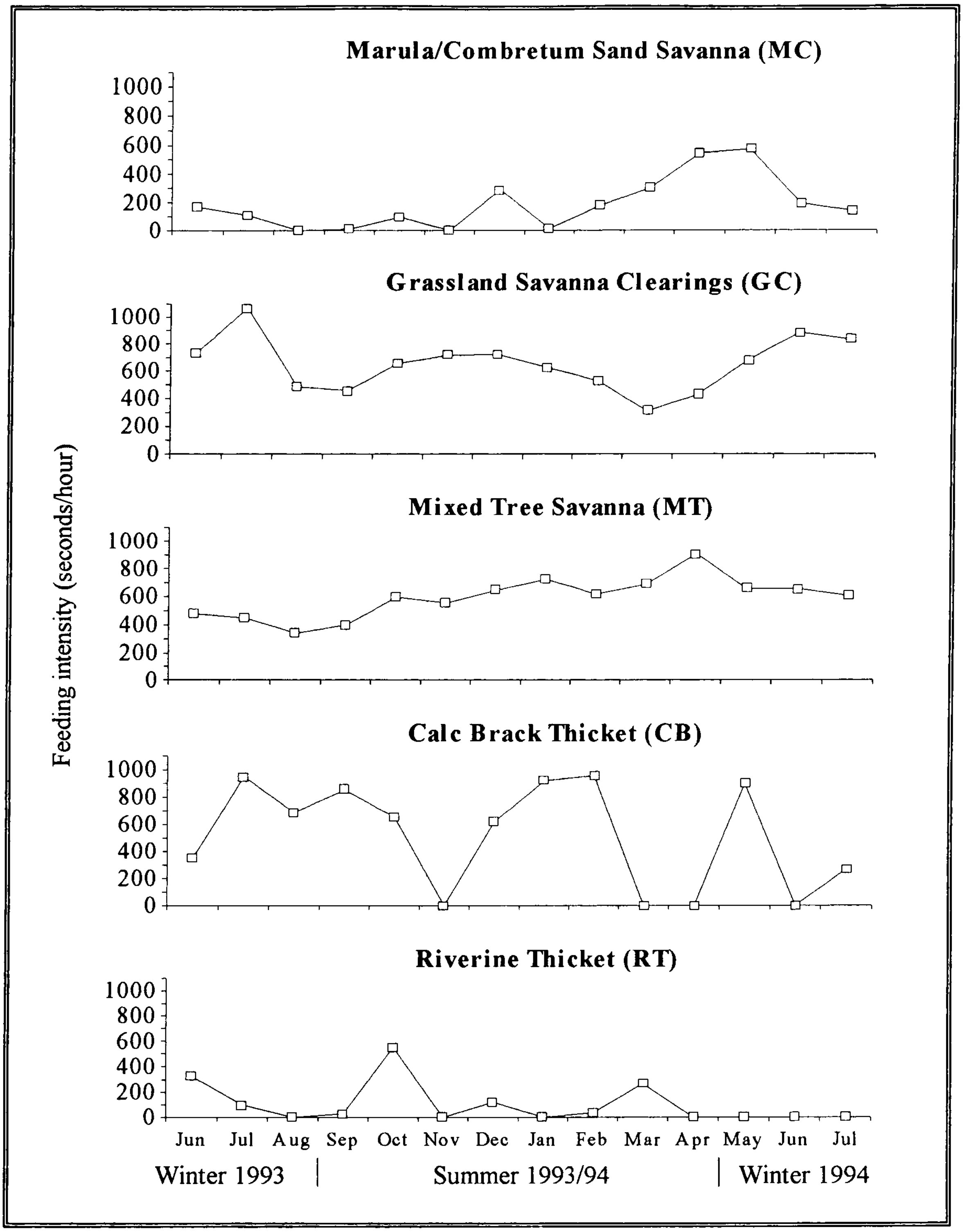


**Fig. 5.5.** The seasonal variation of the feeding intensity recorded in the five different habitat types.

**Table 5.7.** Seasonal differences in the pangolins' feeding intensity on the various species of ants and termites preyed on in each habitat type.

| Ant and termite species | Mean feeding intensity (seconds/hour) | | | | | | | | | | Total feeding intensity (sec./hr) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MC | | GC | | MT | | CB | | RT | | | |
| | S | W | S | W | S | W | S | W | S | W | S | W |
| *Anoplolepis custodiens* | 192 | 231 | 490 | 690 | 409 | 436 | 568 | 721 | 10 | 103 | 392 | 508 |
| *Myrmicaria natalensis* | 62 | 22 | 29 | 8 | 135 | 18 | 36 | 0.2 | 57 | 14 | 88 | 13 |
| *Camponotus cinctellus* | 8 | 25 | | 87 | 15 | 51 | | | | | 9 | 48 |
| *Polyrhachis schistacea* | 6 | | 1 | | 42 | 8 | 25 | | 112 | 21 | 28 | 4 |
| *Hodotermes mossambicus** | | | 21 | 28 | 7 | 26 | 2 | 19 | 1 | | 8 | 21 |
| *Camponotus* sp.- *maculatus* -group | 1 | 4 | 6 | 0.3 | 9 | 1 | 79 | | 38 | | 16 | 1 |
| *Odontotermes* sp*. | | | 8 | 3 | 2 | 2 | 3 | 2 | 47 | | 4 | 2 |
| *Camponotus congolensis* | | | 2 | | 6 | 0.5 | 2 | | 9 | | 4 | 0.2 |
| *Monomorium junodi* | 4 | | 9 | 2 | 3 | 0.2 | | | | | 4 | 1 |
| *Pheidole* sp. 2 | 1 | | 2 | | 7 | | 4 | | | | 4 | |
| *Trinervitermes rapulum** | | | 0.3 | | 4 | | | | | | 2 | |

**Table 5.7 cont.**

| Ant and termite species | Mean feeding intensity (seconds/hour) | | | | | | | | | | Total feeding intensity (sec./hr) | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | MC | | GC | | MT | | CB | | RT | | | |
| | S | W | S | W | S | W | S | W | S | W | S | W |
| Termitidae* | | | 1 | 3 | | 1 | | 1 | 8 | | 0.5 | 1 |
| *Dorylus badius* | | 6 | | 2 | | | | | | | | 1 |
| *Rhadinotermes coarctatus** | | | 0.3 | | 1 | | | | | | 1 | |
| *Tetramorium longicorne* | | | 0.3 | | 0.4 | | | | | | 0.2 | |
| *Tetramorium weitzeckeri* | | | 2 | | | | | | | | 0.4 | |
| *Ocymyrmex fortior* | | | | | 1 | | | | | | 0.3 | |
| *Crematogaster* sp.- *castanea*-group | 1 | | | | | 0.4 | | | | | 0.2 | 0.2 |
| *Pheidole* sp. 3 | | | | | 0.3 | | | | | | 0.2 | |
| *Aenictus eugenii* | | | | | 0.1 | | | | | | 0.04 | |
| Total feeding intensity | 274 | 288 | 573 | 824 | 640 | 543 | 718 | 742 | 282 | 138 | 562 | 600 |
| Total number of species | 8 | 5 | 14 | 9 | 16 | 11 | 8 | 5 | 8 | 3 | 19 | 12 |
| Total hours observed foraging | 28 | 26 | 33 | 43 | 81 | 61 | 18 | 24 | 6 | 3 | 166 | 156 |

* Termite species

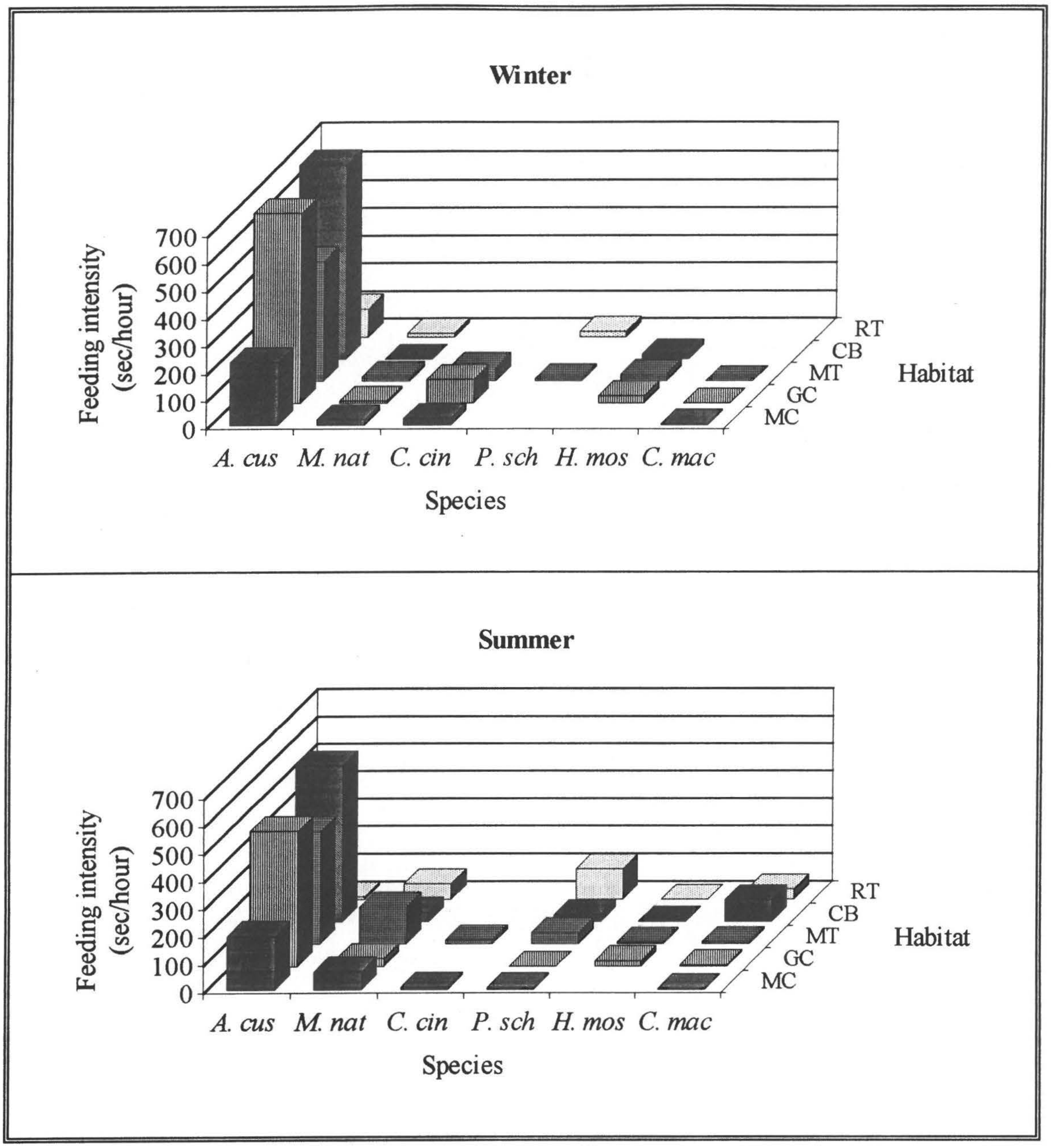


**Fig. 5.6.** The seasonal occurrence of the six most important prey species in the pangolins diet recorded in each habitat type depicted by the pangolins feeding intensity on each species in each habitat type.

was also highest when preying on *A. custodiens,* but only during winter, whereas during summer it was highest when preying on *P. schistacea* (Fig. 5.6; Table 5.7). Thus, *A. custodiens* was the predominant prey species in the marula/*Combretum*, grassland, mixed tree and calc brack habitat types whereas *P. schistacea* predominated in the riverine thicket habitat.

Interestingly, the overall feeding intensity recorded during summer and winter varied by only a small amount despite the large variation of feeding intensities recorded on the various prey species in each habitat type (Table 5.7). Besides a difference in the overall feeding intensity between habitat types there was also an inconsistent seasonal variation in feeding intensity. That is; a higher feeding intensity was recorded during winter than summer in the marula/*Combretum*, grassland and calc brack habitat types, whereas the feeding intensity was higher during summer than winter in the mixed tree and riverine thicket habitat types (Table 5.7).

## DISCUSSION

### Habitat selectivity and utilisation, and the catenary sequence

Habitat selectivity and utilisation have been extensively studied in mammals and it is widely accepted that mammals often select specific habitat types to satisfy their food and shelter requirements. These results confirm that pangolins' are no exception. In general, they appear to rest up in dens usually situated on the crests of hills in marula/*Combretum* habitat or down in the riverine thicket habitat of the valley bottoms (pers. obs.) and then come out during the evening to forage on the slopes.

Approximately 92% of the feedings were recorded on the slopes and the reason for this appears to be related to the soil consistency and vegetation structure of this region. The soils on the slopes have a higher clay content that makes them more structured and thus more easily compacted. This more structured consistency of the soil together with the associated vegetation, particularly *Euclea divinorum* and several of the *Acacia* species, provide an ideal habitat for the nests of the ant species *A. custodiens* and it's Homopteran symbionts (see Discussion of Chapter 3). Since *A. custodiens* contributed to the bulk of the pangolins' diet (77%), they appeared to forage more in areas where this species was more available. This high selectivity for habitats situated on the slopes was the reason for the high habitat selectivity index (*S*) of the pangolins listed in Table 5.2.

Although pangolins foraged mostly on the slopes where the grassland, mixed tree and calc brack habitats were located, there was a considerable seasonal variation in their utilisation of these habitats. During winter feeding bouts were evenly distributed along the slopes with similar proportions of feeding bouts recorded in the grassland, mixed tree and calc brack habitats, whereas during summer they foraged mostly on the footslope with the majority of feeding bouts recorded in the mixed tree habitat.

Although the calc brack habitat contributed to only 3% of the study area and only included in the foraging ranges of three pangolins it was highly selected for by these pangolins during winter. The predominant prey species of pangolins' *A. custodiens* occurred in the highest numbers in this habitat (Table 3.1) and since they were less active and thus occurred in high densities in their underground galleries during winter they could be preyed on more successfully.

Temperature and rainfall are probably the key factors responsible for the seasonal variation in habitat selection by pangolins. An increase in temperature and rainfall during summer is accompanied by an increase in ant activity with the result that ants are less available to pangolins from below the soil surface. This is evident particularly in the calc brack habitat where *A. custodiens* is extremely active during the latter summer months (Fig. 4.10) and particularly after rain (pers. obs.). This appears to be one of the reasons why the pangolins' feeding intensity recorded in the calc brack habitat fell to zero during March and April 1994 (Fig. 5.5). Pangolins may avoid foraging in the calc brack habitat during this period when conditions are less favourable and the density of ants below the soil surface too low.

Another factor that may contribute to this seasonal variation is the water logging of the seep line soils on the upper slopes during the summer rainfall season. These soils remain water logged for part of summer when ant nests in this zone are often flooded as water seeps into them from below the soil surface. As a result of this the ant colonies move and re-establish above or below the seep line zone. This may also be why pangolins foraged more in the marula/*Combretum* habitat above the water logged zone during the end of summer (Fig. 5.1 and Fig. 5.5). Pangolins were observed on several occasions foraging approximately 10 m above an active seep line where water was seeping to the soil surface (pers. obs.).

## Feeding strategy and diet in relation to habitat utilisation

It is interesting that pangolins should vary their feeding strategy according to the habitat and soil type where they forage. This appears to be determined by the composition of species that are preyed on in each habitat type. In the riverine thicket habitat type for example, pangolins' preyed predominantly on *P. schistacea* during summer and *A. custodiens* during winter (Table 5.7; Fig. 5.6). During summer they are able to dig deeper when the soil is softer and thus gain access to the deeper nests of *P. schistacea,* whereas during winter when the soil was harder and *P. schistacea* less available they preyed mostly on the shallower nesting *A. custodiens*. Thus, since the soil was softer in the riverine areas the mean depth of the digs was deeper and the mean duration of feeding bouts longer than those recorded in the other four habitat types (also see discussion in Chapter 4). Conversely, when pangolins foraged in the calc brack habitat type, where the soil was hard and compacted, they preyed mainly on *A. custodiens* (Table 5.7; Fig. 5.6). Thus, the mean depth of the digs were shallower and the mean duration of feeding bouts shorter in the calc brack habitat than those recorded in the other habitat types (Table 5.5 and Table 5.6). This suggests that pangolins continually adapt their feeding strategy according to the feeding conditions of the various combinations of prey, soils and habitat types.

# CHAPTER 6

## CONCLUSIONS

Cape pangolins in the Sabi Sand Game Reserve may not be as rare as was previously thought since the number that were identified during this study exceeded all expectations. However, this does not mean they are no longer threatened. The fauna and flora of this area are protected against hunting, deforestation, farming practices and urbanisation, whereas areas outside nature reserves are not protected and are thus vulnerable to human exploitation. Thus the density of pangolins in areas neighbouring the Sabi Sand Game Reserve is probably considerably lower than within the reserve. A detailed knowledge of pangolins basic habitat requirements within their natural environment is a prerequisite for establishing their status within these unprotected areas.

One of the pangolin's most important basic habitat requirements is food, and their feeding requirements appeared to be determined mainly by ant and termite prey availability. The prey availability was in turn determined by several abiotic and biotic environmental factors. The more important abiotic environmental factors appear to be temperature, light intensity, humidity, rainfall and soil consistency. Biotic factors include; ant and termite species composition, abundance, densities, activity patterns, nesting behaviour and their associations with specific plant species that provided them with food and attract honeydew producing homopteran mutualists.

The pugnacious ant *A. custodiens* is the predominant prey species in the pangolin's diet in the Sabi Sand Game Reserve, and probably most of the Eastern Lowveld. Although they are not the most common ant in the area they are the most favoured species since they occur in relatively high densities close to the soil surface. Thus, compared to the other prey species in the area they are more accessible to pangolins with the result that less effort is required to extract and feed on them. In addition, the shallow tunnelling behaviour of *A. custodiens* makes it easier for pangolins to locate their underground chambers. Since pangolins rely on their keen olfactory sense to locate their prey beneath the soil surface, many of the deep nesting species of ants, and particularly termites, probably go unnoticed during their foraging excursions.

The predominantly diurnal activity of *A. custodiens* also makes them more freely available as prey to the nocturnal pangolins. *A. custodiens* are less active at night and thus congregate in higher densities in their underground galleries where they are available to pangolins. During the day these ants disperse from their galleries while foraging and tending homopterans for honeydew. In addition they often nest in open areas exposed to the sun and ants remaining underground apparently move deeper to escape the hot temperatures close to the soil surface (pers. com. H.G. Robertson, S.A. Museum, P.O. Box 61, Cape Town, 8000).

Although *A. custodiens* are found in most habitat types in the study area they are not uniformly distributed. They appear to have two important basic habitat requirements: (a) a soil medium that is compacted and relatively structured with a clay/loam consistency; and (b) plant species that can provide them with honeydew or support honeydew producing Homopterans. The optimal soils and vegetation structures are usually situated along the slopes of hills and this is where pangolins spent most of their time foraging. The ideal habitat type for *A. custodiens* is the calc brack thicket areas on sodic soils. Pangolins whose ranges included this habitat type spent a relatively high proportion of their time foraging in these areas, especially during winter. Interestingly, while pangolins were out foraging in calc brack thicket areas they were often observed walking from one *Euclea divinorum* shrub to the next searching for and feeding from the nests of *A. custodiens* situated at the base of these shrubs (pers. obs). *E. divinorum* shrubs are often infested with homopterans and a colony of *A. custodiens* is often found nesting around the roots (pers. obs.). When the ants are active they swarm all over the shrub in search of the homopterans that provide them with honeydew (pers. obs.).

Most of the major and median workers in a colony of *A. custodiens* hibernate during winter and the majority of these individuals become repletes with fat ladened abdomens (Steyn 1954). They function as living containers of stored food provisions for the colony during winter. Thus these should be sought after by pangolins since they are high in nutritional value.

Pangolins can not effectively increase their external insulation through piloerection since they have a protective coat of scales rather than fur. For this reason they probably lose more heat and expend more energy during winter than summer. An additional energetic burden is placed on females that are pregnant, and they may be pregnant for most of the winter. Thus, this energy rich food source would be advantageous to pangolins as a supplement to cope with the additional heat loss and energy requirements during winter. Pangolins were occasionally observed feeding on repletes when they were dropped from the mouth at the feeding site, however, it was not possible to measure what proportion they were actually swallowing. Interestingly, there was no significant difference between winter and summer in the pangolins feeding intensity (feeding time in sec/hour) or their overall feeding time. Pangolins preyed almost exclusively on *A. custodiens* during winter and probably did not need to feed for longer or more often since a considerable proportion of the ants they consumed were probably fat ladened repletes.

The overall activity of ants and termites was considerably less during winter compared to summer and that of *A. custodiens* was approximately 11 times lower during winter compared to summer. Thus *A. custodiens* appeared to be more available to pangolins during winter since they were less active above ground and more densely aggregated in their underground galleries. Although this seasonal variation was reflected by an 11% increase of *A. custodiens* in the pangolins diet during winter, this may also be a response to a lower availability of other prey species. For example, *M. natalensis* made up 16% of their diet during summer and only two per cent during winter. Thus the seasonal variation is probably a combination of the variation in availability of all species, or at least the more important species, and possibly a preference for particular species.

Several factors determine prey availability, and since many are inter-linked, it is often difficult to isolate individual factors. For example, the activity patterns, abundance and densities of ants at a given time and location, could be determined by a combination of several factors viz. temperature; light intensity; humidity; moisture levels; inter- and intra-specific competition; soil consistency; and vegetation structure. However, in the present study temperature appeared to be the predominant factor that determined the availability of ants and termites to pangolins. Several species of ants, *A. custodiens* included, move away from the soil surface when temperatures are extreme (pers. com. H.G. Robertson, S.A. Museum, P.O. Box 61, Cape Town, 8000), a behaviour that appears to limit the pangolin's distribution. Thus, although *A. custodiens* is a widespread and a relatively abundant ant species occurring throughout South Africa, it is not necessarily available to pangolins throughout the year. Winter minimum temperatures in the Sabi Sand Game Reserve are usually mild and although they occasionally drop below five degrees Celsius, this usually lasts for only a few days. In contrast, many of the temperate regions of South Africa above the great escarpment experience cold winters where the temperature often falls below five degrees and even below zero. The ants escape the cold by hibernating deep below the soil surface where they are out of reach of the shallow digging pangolin. Thus these extended periods of cold would leave the pangolins without food for long periods during winter.

Although temperature appears to restrict the pangolin's distribution in the southern limit of their range, it is probably not a limiting factor to the north of their distribution, near the equatorial regions of Africa. Rainfall and soil conditions may be more important in determining prey availability in these areas. According to Kingdon (1971) Cape pangolins occurring in East Africa are found in areas where the soil is relatively dry and hard in comparison to the moist habitat of the giant pangolin. Thus, since they are not as well adapted as the giant pangolin for efficient digging, their survival depends on their ability to find an adequate supply of ants and termites close to the soil surface. Cape pangolins in this region appear to prey more on termites and were often observed scratching for termites in animal dung and pieces of wood (Kingdon 1971). The only ants occurring in their diet that was mentioned by Kingdon (1971) were cocktail ants of the genus *Crematogaster*. They often nest in the hollows of branches in trees or in dead wood. Thus it appears that Cape pangolins in this region may feed more superficially than those occurring in South Africa.

One of the most interesting findings of this research was the highly significant interspecies correlation between the duration of the pangolins feeding bouts and the depth of the feeding digs. The first impression one gets is that pangolins spend more energy digging for a greater reward that results in longer feedings. However, pangolins usually feed from shallow digs of only a few centimetres deep. In addition, the difference between the depth that pangolins dig when feeding on the different species may be as little as one centimetre. This difference would be negligible in terms of energy expenditure.

The prey value theory suggested in the present study (Discussion of Chapter 4) appears to be feasible since the ant species that appeared higher in prey value were indeed preyed on for longer with deeper digs. However the one draw back of this theory is that the prey value was estimated subjectively and no quantitative data is available on the prey value of the various species of ants and termites that were used in the correlation (Fig. 4.15). Thus further research is necessary to support this theory. This correlation has not been reported for any of the other terrestrial myrmecophages. Since several of the terrestrial myrmecophages feed in a similar way to pangolins, particularly the ecological equivalents of the Cape pangolin, it would be interesting to establish whether their feeding strategy is also represented by a similar correlation.

# REFERENCES

ACOCKS, J.P.H. 1988. Veld Types of South Africa, 3rd edn. *Mem. Bot. Surv. S. Afr.* 57.

ANDERSEN, A.N. 1983. Species diversity and temporal distribution of ants in the semi-arid mallee region of north-western Victoria. *Aust. J. Ecol.* 8: 127-137.

ANDERSON, A.N. 1986. Diversity, seasonality and community organization of ants at adjacent heath and woodland sites in South-Eastern Australia. *Aust. J. Zool.* 34: 53-64.

ANDERSON, G.D. & TALBOT, L.M. 1965. Soil factors affecting the distribution of the grassland types and their utilization by wild animals on the Serengeti Plains, Tanganyika. *J. Ecol.* 53: 33-56.

ANON 1994. CITIES Anual Reports: *Manis* spp., 1980-1992. Unpublished report. World Conservation Monitoring Centre, Cambridge.

ASHTON, D.H. 1979. Seed harvesting by ants in forests of *Eucalyptus regnans* F. Muell. in central Vivtoria. *Aust. J. Ecol.* 4: 265-267

BAARS, M.A. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* 41: 25-26.

BARBOUR, M.G., BURK, J.H. & PITTS, W.D. 1987. *Terrestrial plant ecology.* The Benjamin/Cummings Publishing Company, California.

BEQUAERT, J. 1922. Ants in their diverse relations to the plant world. *Bull. Amer. Mus. Nat. Hist.* 45: 333-584.

BERGER, W.H. & PARKER, F.L. 1970. Diversity of planktonic Foraminifera in deep sea sediments. *Science* 168: 1345-1347.

BOND, W.J. & SLINGSBY, P. 1983. Seed dispersal by ants in shrublands of the Cape Province and its evolutionary consequences. *S. Afr. J. Sci.* 79: 231-233.

BOTHA, T.C. & HEWITT, P.H. 1978. Influence of diets containing green material on laboratory colonies of *Hodotermes mossambicus* (Hagen). *Phytophylactica* 10: 93-97.

BRÄUTIGAM, A., HOWES, J., HUMPHREYS, T. & HUTTON, J. 1994. Recent information on the status and utilization of African pangolins. *TRAFFIC Bulletin* 15(1): 15-22.

BRIAN, M.V. 1964. Ant distribution in a southern English heath. *J. Anim. Ecol.* 33: 451-461.

BRIAN, M.V. & BRIAN, A.D. 1951. Insolation and ant population in the west of Scotland. *Trans. R. Ent. Soc. Lond.* 102: 303-330.

BRIESE, D.T. & MACAULEY, B.J. 1980. Temporal structure of an ant community in semi-arid Australia. *Aust. J. Ecol.* 5: 121-134.

BRIGGS, J.B. 1961. A comparison of pitfall trapping and soil sampling in assessing populations of two species of ground beetles (Col: Carabidae) *Rep. E. Mall. Res. Sta. 1960* : 108-112.

BRISTOW, J.W. & VENTER, F.J. 1986. Notes on the Permian to Recent geology of the Kruger National Park. *Koedoe* 29: 85-104.

BUCKLEY, R. 1982. *Ant-plant interactions in Australia.* Junk Press. The Hague.

BUITENDAG, E. 1973. The vegetation of the lowveld. *J. Bot. Soc. S. Afr.* 59: 45-50.

BYERS, C.R., STEINHORST, R.K. & KRAUSMAN, P.R. 1984. Clarification of a technique for analysis of utilization-availability data. *J. Wildl. Manage.* 48: 1050-1053.

CALABY, J.H. 1960. Observations on the banded ant-eater *Myrmecobius f. fasciatus* Waterhouse (Marsupialia), with particular reference to its food habits. *Proc. Zool. Soc. Lond.* 135: 183-207.

COLE, A.C. 1934. An ecological study of the ants of the southern desert scrub region of the United States. *Ecology* 9: 388-405.

COULSON, I. 1989. The pangolin (Manis temminckii Smuts, 1835) in Zimbabwe. *Afr. J. Ecol.* 27: 149-155.

DORST, J. & DANDELOT, P. 1970. *A field guide to the larger mammals of Africa.* Collins, London.

DYE, P.J. & WALKER, B.H. 1980. Vegetation-environment relations on sodic soils of Zimbabwe Rhodesia. *J. Ecol.* 68: 589-606.

FRIEND, T. 1982. The numbat - an endangered specialist. *Aust. Nat. Hist.* 20: 339-342.

FUNSTON, P.J. 1992. *Movements, habitat selection and population structure of buffalo (Syncerus caffer caffer Sparrman) in the Sabi Sand Wildtuin.* MSc thesis, University of Pretoria.

GERTENBACH, W.P.D. 1980. Rainfall patterns in the Kruger National Park. *Koedoe* 23: 35-43.

GREENSLADE, P. & GREENSLADE, P.J.M. 1971. The use of baits and preservatives in pitfall traps. *J. Aust. Ent. Soc.* 10: 253-260.

GREENSLADE, P.J.M. 1964. Pitfall trapping as method for studying populations of Carabidae (Coleoptera). *J. Anim. Ecol.* 33: 301-310.

GREENSLADE, P.J.M. 1971. Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. *J. Appl. Ecol.* 8: 323-352.

GREENSLADE, P.J.M. 1973. Sampling ants with pitfall traps: digging-in effects. *Insectes Soc.* 20: 343-353.

GREENSLADE, P.J.M. 1979. *A guide to ants of South Australia.* South Australian Museum, Adelaide.

GREENSLADE, P.J.M. & GREENSLADE, P. 1977. Some effects of vegetation cover and disturbance on a tropical ant fauna. *Insectes Soc.* 24: 163-182.

GREENSLADE, P.J.M. & GREENSLADE, P. 1984. *Soil surface insects of the Australian arid zone*. Proc. Sesquicentennial Conf. Arid Australia. Australian Museum, Sydney.

GRIFFITHS, M. & SIMPSON, K.G. 1966. A seasonal feeding habit of spiny anteaters. *CSIRO wildl. Res.* 11: 137-143.

HARTWIG, E.K. 1965. Die nesstelsel van die grassdraertermiet *Hodotermes mossambicus* (Hagen) (Isoptera) en aspekta rakende bestryding. *Suid-Afrikaanse Tydskrif vir Landbouwetenskap* 8: 643-660.

HAYASHIDA, K. 1960. Studies on the ecological distribution of ants in the Sapporo and its vicinity. *Insectes Soc.* 7: 125-162.

HAYES, W.B. 1970. The accuracy of pitfall trapping for the sand beach isopod *Tylos punctatus. Ecology* 51: 514-516.

HOLT, S.J. 1970. On the foraging activity of the wood ant. *J. Anim. Ecol.* 24: 1-34.

HUNTLEY, B.J. 1984. Characteristics of South African biomes. In: *Ecological effects of fire in South African ecosystems* (Eds. Booysen, P. de V. & Tainton, N.M.), Springer Verlag, Berlin. pp. 2-17.

HULBERT, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52: 577-586.

JACOBSEN, N.H.G., NEWBERY, R.E., DE WET, M.J., VILJOEN, P.C. & PIETERSON, E. 1991. A contribution of the ecology of the Steppe pangolin *Manis temminckii* in the Transvaal. *Z. Saugetierkunde* 56: 94-100.

JENNINGS, D.T., HOUSEWEART, M.W. & DUNN, G.A. 1986. Carabid beetles (Coleoptera: Carabidae) associated with strip clearcut and dense spruce-fir forests of Maine. *Coleopts. Bull.* 40: 251-263.

JOOSSE, E.N.G. 1965. Pitfall trapping as a method for studying surface dwelling Collembola. *Z. Morph. Okol. Tiere* 55: 587-596.

KINGDON, J. 1971. *East African mammals.* An atlas of evolution. Vol. I. Academic Press, London & New York.

KINGDON, J. 1984. *East African mammals.* Vol. I. University of Chicago Press, Chicago.

KOEN, J.H. & BREYTENBACH, W. 1988. Ant species richness of fynbos and forest ecosystems in the southern cape. *S. Afr. J. Zool.* 23: 184-188.

LATHWELL, D.J. & GROVE, T.L. 1986. Soil-plant relationships in the tropics. *Ann. Rev. Ecol. Syst.* 17: 1-16.

LOUW, J.F. 1968. Die ekologie van die malmier, *Anoplolepis custodiens* (Smith) (Hymenoptera: Formicidae), in die sentrale Oranje-Vrystaat - 1. Die bogrondse aktiewiteitspeil van die werkers. *J. Ent. Soc. Sth. Afr.* 31: 241-248.

LUBIN, Y.D. & MONTGOMERY, G.G. 1981. Defenses of Nasutitermes termites (Isoptera, Termitidae) against Tamandua ant-eaters (Edentata, Myrmecophagidae). *Biotropica* 13: 66-76.

LUBIN, Y.D., MONTGOMERY, G.G. & YOUNG, O.P. 1977. Food resources of ant-eaters (Edentata: Myrmecophagidae) 1. A year's census of arboreal nests of ants and termites on Barro Colorado Island, Panama canal zone. *Biotropica* 9: 26-34.

LUFF, M.L. 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* 19: 345-357.

MACARTHUR, R.H. & MACARTHUR, J. 1961. On bird species diversity. *Ecology* 42: 594-598.

MAJER, J.D. 1972. The ant mosaic in Ghana cocoa farms. *Bull. Ent. Res.* 62: 151-160.

MAJER, J.D. 1978. An improved pitfall trap for sampling ants and other epigaeic invertebrates. *J. Aust. Ent. Soc.* 17: 261-262.

MAJER, J.D. 1980. The influence of ants on broadcast and naturally spread seeds in rehabilitated bauxite mined areas. *Reclamation Review* 3: 3-9.

MARSH, A.C. 1984. The efficacy of pitfall traps for determining the structure of a desert ant community. *J. ent. Soc. Sth. Afr.* 47: 115-120.

MARSH, A.C. 1986. Ant species richness along a climatic gradient in the Namib desert. *J. Arid Environ.* 11: 235-241.

MARTIN, P. & BATESON, P. 1986. *Measuring behaviour: An introductory guide.* Cambridge University Press.

McGREW, W.C. 1983. Animal foods in the diets of wild chimpanzees (*Pan troglodytes*): Why cross-cultural variation? *J. Ethol.* 1: 46-61.

McNAUGHTON, S.J. 1978. Serengeti ungulates: feeding selectivity influences the effectiveness of plant defence guilds. *Science* 199: 806-807.

MELTON, D.A. 1976. The biology of the aardvark (Tubulidentata - Orycteropodidae. *Mammal Rev.* 6: 75-88.

MOHR, E. 1961. *Schuppentiere. Die Neue Brehm Bücherei.* Vol. 284. Ziemsen, Wittenberge-Lutherstadt.

MORRISON, C.G.T., HOYLE, A.C. & HOPE-SIMPSON, J.F. 1948. Tropical soil-vegetation catenas and mosaics - a study in the S.W. part of Anglo-Egyptian Sudan. *J. Ecol.* 36: 1-84.

MURDOCH, W.W., EVANS, F.C. & PETERSON, C.H. 1972. Diversity and pattern in plants and insects. *Ecology* 53: 819-829.

NEL, J.A.J. 1978. Notes on the food and foraging behavior of the bat-eared fox, *Otocyon megalotis. Bull. Carneg. Mus. nat. Hist.* 6: 132-137.

NEL, J.J.C. & HEWITT, P.H. 1969. A study of the food eaten by a field population of the harvester termite, *Hodotermes mossambicus* (Hagen) and its relation to population density. *J. ent. Soc. sth. Afr.* 32: 123-131.

NEU, C.W., BYERS, C.R. & PEEK, J.M. 1974. A technique for analysis of utilization-availability data. *J. Wildl. Manage.* 38: 541-545.

OHIAGU, C.E. 1979. A quantitive study of seasonal foraging by the grass harvesting termite, *Trinervitermes geminatus* (Wasmann), (Isoptera, Nasutitermitinae) in southern Guinea savanna, Mokwa, Nigeria. *Oecologia* 40: 179-188.

PIANKA, E.R. 1967. On lizard species diversity: North American flatland deserts. *Ecology* 48: 333-351.

PIELOU, E.C. 1966. The measurement of diversity in different types of biological collections. *J. Theoret. Biol.* 13: 131-144.

REDFORD, K.H. 1983. Mammalian myrmecophagy: Feeding, foraging and food preference. D.Phil. thesis, Harvard University Cambridge, Massachusetts.

REDFORD, K.H. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. *J. Zool. Lond.* 203: 385-395.

REDFORD, K.H. 1985a. Feeding and food preference in captive and wild giant ant-eaters (*Myrmecophaga tridactyla*). *J. Zool. Lond.* 205: 559-572.

REDFORD, K.H. 1985b. Food habits of armadillos (Xenarthra: Dasypodidae), In: *Ecology and Evolution of Sloths, Anteaters and Armadillos (Mammalia, Xenarthra = Edentata)* (ed. G.G. Montgomery), Smithsonian institute press, Washington, D.C. pp. 429-437.

REDFORD, K.H. 1987. Ants and termites as food: patterns of mammalian myrmecophagy. In: *Current Mammalogy*. Vol I. Genoways, H.H. (Ed.). Plenum Press, New York.

RICHARDSON, P.R.K. 1987a. Food consumption and seasonal variation in the diet of the aardwolf *Proteles cristatus* in Southern Africa. *Z. Säugetierkunde* 52: 307-325.

RICHARDSON, P.R.K. 1987b. Aardwolf: The most specialized myrmecophagous mammal? *S. Afr. J. Sci.* 83: 643-646.

ROOM, 1975. Diversity and organization of the ground foraging ant faunas of forest, grassland and tree crops in Papua New Guinea. *Aust. J. Zool.* 23: 71-89.

RUSSEL, E.W. 1973. *Soil conditions and plant growth,* 10th edn. Longman, London.

SAMWAYS, M.J. 1981. Comparison of ant community structure (Hymenoptera: Formicidae) in citrus orchards under chemical and biological control of red scale, *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae). *Bul. Ent. Res.* 71: 663-670.

SAMWAYS, M.J. 1983. Community structure of ants (Hymenoptera: Formicidae) in series of habitats associated with citrus. *J. Appl. Ecol.* 20: 833-847.

SAMWAYS, M.J., NEL, M. & PRINS, A.J. 1982. Ants (Hymenoptera: Formicidae) foraging in citrus trees and attending honey-dew producing Homoptera. *Phytophylactica* 14: 155-157.

SANDERS, C.J. 1972. Seasonal and daily activity patterns of carpenter ants (*Camponotus* spp.) in northwestern Ontario (Hymenoptera: Formicidae). *Can. Entomol.* 104: 1861-1867.

SANDS, W.A. 1961. Foraging behaviour and feeding habits in five species of *Trinervitermes* in West Africa. *Ent. exp. appl.* 4: 277-288.

SCHOENER, T.W. 1974. Resource partitioning in ecological communities. *Science (Wash. D.C.)* 185: 27-39.

SHANNON, C.E. & WEAVER, W. 1949. *The mathematical theory of communication.* University of Illinois Press, Urbana.

SIH, A. 1980. Optimal foraging: partial consumption of prey. *Am. Nat.* 116: 281-290.

SKAIFE, S.H. 1979. *African insect life.* Revised edition. Struik, Cape Town.

SMITHERS, R.H.N. 1983. *The Mammals of the Southern African subregion.* University of Pretoria, Pretoria.

SMITHERS, R.H.N. 1986. *South African Red Data Book - terrestrial mammals.* South African National Scientific Programs Report 125. Council for Scientific and Industrial Research, Pretoria.

SOUTHWOOD, T.R.E. 1978. *Ecological Methods.* Chapman and Hall, New York.

STEYN, J.J. 1954. The pugnatious ant *Anoplolepis custodiens* (Smith) and its relation to the control of citrus scales at Letaba. *Mem. Ent. Soc. S. Afr.* No. 3: 1-96.

STRANG, R.M. 1982. Some man-made changes in successional trends on the Rhodesian Highveld. *J. Appl. Ecol.* 2: 249-256.

SWART, J.M. 1992. Home range and foraging behaviour of the pangolin (*Manis temminckii* Smuts, 1835) in the Sabi Sand Wildtuin. Unpublished B.Sc. (Hons.) thesis, University of Pretoria.

SWEENEY, R.C.H. 1956. Some notes on the feeding habits of the ground pangolin, *Smutsia temminckii* (Smuts). *Ann. Mag. Nat. Hist. 12th ser.* 9: 893-896.

SWEENEY, R.C.H. 1973. *Background of Baobabs*. London: Constable and Co.

TINLEY, K.L. 1979. Management ecology of the Sabi-Sand Wildtuin. (Unpubl. report).

TYSON, P.D. & DYER, T.G.J. 1975. Mean annual fluctuations of precipitation in the summer rainfall region of south Africa. *S. Afr. Geogr. J.* 57:104-110

VAN EE, C. 1978. Pangolins can't be bred in captivity. *African Wildlife* 32(4): 24-25.

VENTER, F.J. 1986. Soil patterns associated with the major geological units of the Kruger National Park. *Koedoe* 29: 125-138.

VENTER, F.J. & BRISTOW, J.W. 1986. An account of the geomorphology and drainage of the Kruger National Park. *Koedoe* 29: 117-124.

WALRAVEN, F. 1983. The Timbavati gabbro of the eastern transvaal lowveld - a probable example of Hertzian fracturing. *Ann. Geol. Surv. S. Afr.* 17: 21-27.

WASER, P.M. 1980. Small nocturnal carnivores: ecological studies in the Serengeti. *Afr. J. Ecol.* 18: 167-185.

WEBER, N.A. 1943. The ants of the Imatong mountains, Anglo Egyptian Sudan. *Bull. Mus. Comp. Zool. Harv.* 93: 263-389.

WEST, O. 1947. Thorn bush encroachment in relation to the management of veld grazing. *Rhod. J. Agric. Res.* 64: 488-497.

WHITFORD, W.G. 1978. Structure and seasonal activity of Chihuahua desert ant communities. *Insectes Soc.* 25: 79-88.

WHITTAKER, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 21: 213-251.

WILLIS, C.K., SKINNER J.D. & ROBERTSON H.G. 1992. Abundance of ants and termites in the false Karoo and their importance in the diet of the aardvark *Orycteropus afer*. *Afr. J. Ecol.* 30: 322-334.

WILSON, D.S. & CLARK, A.B. 1977. Above ground predator defence in the harvester termite, *Hodotermes mossambicus* (Hagen). *J. ent. Soc. S. Afr.* 40: 271-282.

YEATMAN, E.M. & GREENSLADE, P.J.M. 1980. Ants as indicators of habitat in three conservation parks in south Australia. *S. A. Nat.* 55: 20-26; 30.