

https://dspace.org/

The biology and relationships of the ground woodpecker

Oatley, Terence Barry

1992
https://hdl.handle.net/10539/27820

Downloaded from a DSpace repository. https://dspace.org/

THE BIOLOGY AND RELATIONSHIPS OF THE GROUND WOODPECKER

T. B. OATLEY

University of the Witwatersrand
1992

THE BIOLOGY AND RELATIONSHIPS OF THE GROUND WOODPECKER

Terence Barry Oatley

A thesis submitted to the Faculty of Science,
University of the Witwatersrand, Johannesburg,
in fulfilment of the requirements for the degree
of Doctor of Philosophy.

Cape Town, 1992.

ABSTRACT

Paterson's recognition concept of species predicts that new species arise as an incidental consequence of adaptation by small, isolated populations to a new environment. If this is so, species-wide characteristics, especially those of the species fertilization system, should have evolved entirely in isolation and should relate strongly to the normal habitat of the species. The purpose of this study is to explore and test this theory. The African Ground Woodpecker Geocolaptes olivaceus is the tool for this exploration. The first phase of the study documents aspects of ecology, behaviour and breeding biology of this little-studied bird; the second phase establishes its relationship to other African woodpeckers, and in the third phase a hypothetical account of a speciation event is presented.

The Ground Woodpecker is the only terrestrial picid on the African continent and its distribution is confined to the subcontinent south of the Tropic of Capricorn. It is seldom found far from rocks and boulders; these provide the birds with resting and hiding places and display platforms. The birds excavate tunnels in earthen banks for roosting and nesting.

Field studies reveal that the Ground Woodpecker spends about one third of the daylight hours foraging, leaving the roost tunnel very early. Long periods are spent resting on the rocks, the birds usually orienting to direct sunlight. Ground Woodpeckers eat ants and 53 species of 24 genera have been recorded as prey. Small beetles and termites may be accidentally ingested.

The species is easily heat-stressed and seeks shade in warm weather. It has well-developed predator-avoidance behaviour and is particularly wary of avian predators. Sentinel birds are a regular feature of foraging groups. Ground Woodpeckers remain together as family groups from the time the young fledge until the onset of the following breeding season. Groups of up to six birds have been

observed; the usual group size is of three birds. All birds in a group roost together in a single tunnel and nocturnal defaecation is inhibited. Pairs or groups habitually occupy areas of from 21 ha to 70 ha but may range over areas of up to 250 ha.

Two theories of relationship have been proposed, placing Geocolaptes close to the genus Campethera on the one hand or to the genus Mesopicos on the other. This study reveals, however, that the Ground Woodpecker shares several characters with the Bearded Woodpecker Thripias namaquus, and Boolean factor analysis of an array of character states suggests that it is more closely related to this species than to any other. A cladistic analysis places Geocolaptes and Thripias in the same monophyletic taxon and an appraisal of theoretically possible phylogenetic trees suggests that the Bearded Woodpecker is probably the living ancestor of the Ground Woodpecker.

An hypothesis of origin of the Ground Woodpecker is presented, showing how and where an ancestral population of Bearded Woodpeckers could have become isolated in a treeless environment. The same scenario is used to show how natural selection, operating on individuals within a precise framework of habitat constraints, would have resulted in a new set of species-wide characteristics.

Paterson's recognition concept proved entirely adequate for the hypothetical reconstruction of this speciation event, but the origin and adaptations of the Ground Woodpecker can not be credibly explained in terms of alternative models of speciation.

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

F. B. Ochse

29 day of March, 1993.

To Polly, Mark, Jenny, Ruth and Michael,
for the gift of all the hours that they
might otherwise have shared with me.

TABLE OF CONTENTS

		Page
PREFACE		viii
Chapter		
1	INTRODUCTION	1
2	DISTRIBUTION, HABITAT, TAXONOMY AND STUDY AREAS	11
	Distribution	11
	Habitat	11
	Taxonomy	14
	Study areas	15
3	DIURNAL ACTIVITY AND BEHAVIOURAL THERMOREGULATION	23
	Introduction	23
	Methods	23
	Results	24
4	DIET AND FEEDING HABITS	37
	Introduction	37
	Methods	37
	Results	40
	Summary	55
5	SIGNAL BEHAVIOUR	57
	Introduction	57
	Vocalizations	58
	Displays	61
	Predator avoidance behaviour	68
	Discussion	75
6	BREEDING BIOLOGY AND GROUP SIZE	80
	Introduction	80
	Tunnel excavation	80
	Nest tunnel sites	82
	Alledged use of nesting material	83
	Eggs	84
	Incubation	85
	Parental care and fledging behaviour	85
	Alledged communal breeding	89
	Group size	90
	Summary	94

TABLE OF CONTENTS (cont.)

Chapter		page
7	RELATIONSHIPS OF *Geocolaptes*	96
	Introduction	96
	Existing hypotheses	98
	Tongue morphology	101
	The fossil record	104
	Derived character states	106
	Phylogeny	113
8	ANCESTRY AND ORIGIN	120
	Introduction	120
	Potential ancestors	120
	Outline of habits and ecology of Bearded Woodpecker	123
	Modes of speciation	124
	Hypothetical scenario for the origin of *Geocolaptes*	126
	Discussion	137
9	ADAPTATION AND ITS CONSEQUENCES	14[illegible]
	Introduction	14[illegible]
	The environment	14[illegible]
	Directional selection	14[illegible]
	Consequences	14[illegible]
	Selection and genetic variance	14[illegible]
	Speciation	1[illegible]
	Models of speciation	1[illegible]
	Conclusions	15[illegible]
REFERENCES		162

PREFACE

The nature and origin of species is of fundamental importance to population biology. The problem of how new species arise is currently one of the most contentious issues in evolutionary theory. There is increasing support for the notion that changing environments play a critical role in lineage splitting, and in the African continent the alternation of forest and savanna habitats may have been a key factor in the origin of Homo sapiens. The Ground Woodpecker seems likely to have been a product of the same type of event. The aim of this study has been to identify the adaptations of this species and to use this knowledge to provide insight into its origin.

The potential suitability of the Ground Woodpecker for a study of this nature was long ago realised by Prof. H.E.H. Paterson. It has been my privilege and challenge to bring this study to fruition. Any success I have achieved has been due in large measure to the constant encouragement and advice which Hugh Paterson has provided, not only during the period of this research but throughout the 32 years of our acquaintance.

I was much helped by Dr Elizabeth Vrba, formerly of the Transvaal Museum, Pretoria, who packed very stimulating guidance into a few hours of discussion at a critical stage of this study. Dr André Prins (now retired) of the South African Museum in Cape Town gave freely of his expertise to identify woodpecker-mangled ants and a by-product of this study is the discovery of at least two ant species new to science. Dr Roy Earlé, formerly of the National Museum, Bloemfontein, has contributed much field data and many samples, and shown me the haunts of Ground Woodpeckers in the Orange Free State. My much-missed friend, the late Dr David Skead, provided continual encouragement and, on a memorable afternoon on Slangkop plateau, enthusiastically supported my contention that members of the local Ground Woodpecker group were exhibiting sentinel behaviour.

Dr N. Passmore of the University of the Witwatersrand provided sonograms of taped woodpecker calls. Ms P. Haarhof of the South African Museum arranged the loan of fossil and other skeletal material. Dr E.A. Ueckermann of the Plant Protection Unit is thanked for the identification of mites. Permission to use the photograph on p. 17 was given by the Estuarine and Coastal Research Unit of the National Institute of Oceanology. Unpublished bird atlas data were made available in the early stages of the study by regional branches of the Southern African Ornithological Society. The more up-to-date distribution map on p. 12 was kindly made available by Mr James Harrison, coordinator of the Southern African Bird Atlas Project.

Many people have contributed observations or assistance in various ways and I wish to thank Dr G. Avery, R.K. Brooke, Dr P.A. Clancey, W.R.J. Dean, J.J. Herholdt, Dr R.S. Knight, Dr D. Kurtz, J. Komen, Ms C. Kay, Dr A. Kemp, Dr I.A.W. Macdonald, P. le S. Milstein, P. Martin, R.,J. & E. Martin, M. Neatherway, S.E. Piper, Mr & Mrs G. Prins, Dr R.P. Prys-Jones, Dr P.G. Ryan, R.K. Schmidt, M.B. Skead, Mrs I. Starck, P. Steyn, Mrs T. Cassidy, W.R. Tarboton, Prof. L.G. Underhill and G. Wright.

Data from Chapters 2, 3, and 4 have been published in the paper:
Oatley, T.B., Earlé, R.A. & Prins, A.J. 1989. The diet and foraging behaviour of the Ground Woodpecker. Ostrich 60: 75-84.

LIST OF TABLES

		Page
1	Total minutes of observation on, and observed foraging by Ground Woodpeckers at Wellington, April to September 1980	28
2	Estimated number of minutes spent foraging in each hour, and percentage of available time used by Wellington woodpeckers	28
3	Perching orientation of Ground Woodpeckers to wind direction in absence of direct sunlight	34
4	List of genera and species of ants found in faeces of Ground Woodpeckers	42
5A	Percentage frequency of occurrence of ant genera and other items found in Ground Woodpecker faeces	43
5B	Diets of neighbouring Ground Woodpecker groups	44
6	Results of surface sampling of ant genera at Elsies Peak	45
7	Ant genera found under stones at Elsies Peak	47
8	Seasonal availability of ant brood and alates at Elsies Peak	47
9	Frequency of area utilization by Ground Woodpecker group at Elsies Peak	5[illegible]
10	Results of ant sampling transects witnin and outside of areas frequented by Ground woodpecker groups	[illegible]
11	Months in which egg laying is commenced by the Ground Woodpecker	[illegible]
12	Monthly variation in the size of Ground Woodpecker groups	[illegible]
13	Recent taxonomic arrangements of Afrotropical woodpeckers	97
14	Dimensions of tarsometatarsus of extant barbet, honeyguide, Wryneck and five woodpeckers compared with fossil picid metatarsi	105
15	List of character states used in factor analysis	109
16	Character representation in Afrotropical woodpecker genera	115
16B	Character representation in Outgroup comparison	116

LIST OF FIGURES

		Page
1	Map of distribution of the Ground Woodpecker	12
2	Views of the Wellington study site	16
3	Aerial view of the Glencairn Valley	17
4	Views of the Castledene study site	19
5	Views of the Slangkop study site	20
6	Histogram of estimated daily distribution of foraging activity at Wellington for the months of April to September	29
7	Perching orientation of Ground Woodpeckers at Wellington	32
8	Favoured hot weather resting site at Castledene	34
9	Map of Ground Woodpecker faecal sampling sites	41
10	Sonograms of Ground Woodpecker calls	59
11	Postures used by Ground Woodpeckers in aggressive encounters	64
12	Adult female Ground Woodpecker approaching and attacking model	66
12D	Alternate foraging and sentinel behaviour by two Ground Woodpeckers	73
13	Tunnels of Ground Woodpeckers at Wellington dam	81
14	Cladogram for five genera of endemic Afrotropical woodpeckers	115
14A	Outgroup comparison; computer generated phylogeny of Colaptes and Afrotropical woodpecker genera	116
15	Phylogenetic hypotheses of ancestry of the Bearded and Ground Woodpeckers	122
16	Distribution of the Bearded Woodpecker	127
17	Probable escape routes of peripheral populations of Bearded Woodpeckers from frost-devastated woodland	136

1. INTRODUCTION

> "They went on with their exercises, each helping the other, till morning came; and when the sun was high they rested and dried themselves. Then they saw that they were both of them quite different from what they had been."
>
> Rudyard Kipling (1902): Just So Stories; The Beginning of the Armadilloes.

In our efforts to understand how the diversity of eukaryotic life on earth has come about, we notice, firstly, that the units of this diversity are species. Secondly, it is an observable fact that members of a species share a number of fixed characters. The most significant of these are:

(a) the characters which, to use Carson's (1957) original, succinct description, "limit the field of gene recombination", that is to say those characters which determine the organisms with which any member of a species can exchange and recombine its genes. These characters are here referred to as the species fertilization system.

(b) The characters that fit members for (and often restrict them to) a particular type of habitat: i.e. the normal habitat of the species.

(c) The characters which determine the manner of existence in the biosphere of all member organisms of the species. (This place is usually referred to as the species' ecological niche, but this term is avoided here, primarily because of its connotation with conventional competition theory and the inherent bias which such interpretations place upon our thinking.) These characters also determine, to some extent, the geographical range of the species.

In terms of Paterson's Recognition concept of species

(1985) one is led to expect that these sets of characters, shared by all member organisms of a particular species, are fixed during speciation, which Paterson believes happens when a small population is isolated in an environment different from that occupied by its parental species. The characters, necessarily different from those of the parental species, arise as a direct result of adaptation (sensu Williams 1966) to the new environment. The restriction to a new habitat-type is what destabilizes the homeostatic characteristics of the original species. The ecological consequences of this proposal have been drawn and discussed by Walter et al. (1984).

How can these ideas be explored?

The foregoing implies that the significant, species-wide character sets concerned with habitat, ecology and fertilization, are all evolved and fixed in a small population restricted to a new habitat. From a different point of view, by comparing pairs of species it can be said that the species are different because their fertilization characters have diverged in adaptation to different habitats. The characters of the fertilization system, a subset of which comprise what Paterson terms the specific-mate recognition system (SMRS), should appear to be appropriate to the species habitat, indicating that they are adaptive characters rather than "effects" sensu Williams (1966). The same applies to the other fixed character sets concerned with habitat and ecology.

By selecting related species pairs it may be possible to test these expectations to some extent. The theory is that the character sets (a,b,c) for each species should relate to the respective normal habitats of those species. Such comparisons will not be very easy if the differences between the normal habitats of species X and Y are small. However, it is not difficult to find an occasional species which appears to have made a dramatic saltation. The families of African birds provide many examples of species with ecological requirements which are notably different from those of other members of their families. As examples

there are the Blackheaded Heron Ardea melanocephala and Cattle Egret Bubulcus ibis, with ecological characteristics distinct from those of most herons; the Hadada Ibis Bostrychia hagedash and Green Ibis Bostrychia rara, raucous, forest-adapted members of a family of otherwise mostly non-vociferous, marsh-frequenting species; the piscivorous owls of Africa, numbering but three of 26 Afrotropical species; several dryland kingfishers that do not eat fish, and a woodpecker that frequents rocks instead of trees.

This last species has clearly been involved in an evolutionary saltation and is potentially a favourable subject to provide a scenario to illustrate Paterson's hypothesis. However, an immediate question is begged: what species can be regarded as a sister species? Although there is no obvious answer to this question, the general characteristics of such a relative could be clearly outlined from the collective properties of other species of woodpeckers. Consequently, it was the African Ground Woodpecker Geocolaptes olivaceus (Gmelin) that was chosen as the test species on which this thesis was to be based. One of the objectives of the study was to determine its closest relative.

The Ground Woodpecker

> "This bird, unlike all other woodpeckers, lives almost entirely on the ground; it is usually to be found only among the rocky boulder-strewn and treeless hills, with which so large a portion of South Africa is covered."
>
> W.L. Sclater (1903).

'Elsies Peak: 20/01/85. Sunny; wind light SE; 17h40-19h25. Group of six GWPs basking on crevice rock at 17h50. One, then two, three, then four sitting on incident sloping western face of rock, the first one virtually throughout period with back to sun and at a full squat on the

rock. Birds sat thus for virtually an hour until about 18h55 when they started to group at top of rock. Interim activity when adult Black Eagle soared in updraft, very high and not directly overhead. GWPs very wary - sky-gazing - sometimes twisting heads as though to see better. More wariness when Rock Kestrel appeared, hanging in updraft from quarry - much lower than eagle, but didn't make a pass at the GWPs. Auto-suggestion evident at times - when one GWP stretched, two or three others did so in quick succession. Preening by one sometimes initiated preening by another, but preening not frequent. One bird sitting on one leg part of time. No evident dominance by any individual. Bird at bottom of group moved to highest position when eagle appeared, but another bird subsequently moved even higher. Could not detect M/F characters at 15 m even though sun full on birds. In final few minutes before flying off, all were in compact group, feathers rather fluffed, making conversational soft burg sounds to each other, almost like growls. Birds flew to neighbouring rock outcrop to east at 19h03 and started to forage there with much peeurg calling. Felt rock face after they had left - distinctly warm to the touch.'

Geocolaptes Swainson is a monotypic genus and there is division of opinion about its probable ancestry and relationship to other African picids. Goodwin (1968) considers, on the basis of general similarity of colour pattern, that the African Ground Woodpecker evolved from stock ancestral also to the Mesopicos goertae - M. griseocephalus superspecies. Short (1980), however, suggests that Geocolaptes evolved from some ancestral species of Campethera with specializations for a ground-living existence.

The African Ground Woodpecker is one of three living terrestrial woodpecker species in the world, the other two occuring respectively in the northern Andes and in the eastern plains of South America. These two are congeneric with six other extant Colaptes species in the New World

rock. Birds sat thus for virtually an hour until about 18h55 when they started to group at top of rock. Interim activity when adult Black Eagle soared in updraft, very high and not directly overhead. GWPs very wary - sky-gazing - sometimes twisting heads as though to see better. More wariness when Rock Kestrel appeared, hanging in updraft from quarry - much lower than eagle, but didn't make a pass at the GWPs. Auto-suggestion evident at times - when one GWP stretched, two or three others did so in quick succession. Preening by one sometimes initiated preening by another, but preening not frequent. One bird sitting on one leg part of time. No evident dominance by any individual. Bird at bottom of group moved to highest position when eagle appeared, but another bird subsequently moved even higher. Could not detect M/F characters at 15 m even though sun full on birds. In final few minutes before flying off, all were in compact group, feathers rather fluffed, making conversational soft burg sounds to each other, almost like growls. Birds flew to neighbouring rock outcrop to east at 19h03 and started to forage there with much peeurg calling. Felt rock face after they had left - distinctly warm to the touch.'

Geocolaptes Swainson is a monotypic genus and there is division of opinion about its probable ancestry and relationship to other African picids. Goodwin (1968) considers, on the basis of general similarity of colour pattern, that the African Ground Woodpecker evolved from stock ancestral also to the Mesopicos goertae - M. griseocephalus superspecies. Short (1980), however, suggests that Geocolaptes evolved from some ancestral species of Campethera with specializations for a ground-living existence.

The African Ground Woodpecker is one of three living terrestrial woodpecker species in the world, the other two occuring respectively in the northern Andes and in the eastern plains of South America. These two are congeneric with six other extant Colaptes species in the New World

and their relationships are thus well known. Because of its wide divergence from other extant African woodpeckers Short (1971a) has stated that "the African Ground Woodpecker is an ancient species." Such a viewpoint is in accordance with the evolutionary model of phyletic gradualism which predicts a pattern of continuous, gradual evolutionary change. The model had not been seriously challenged when Short made this statement. However, an alternative model of punctuated equilibria, subsequently proposed by Eldredge and Gould (1972), predicts short pulses of speciation (by unspecified mode) followed by long periods of stasis. It has been vigorously debated by paleontologists and evolutionary biologists and is gaining wide acceptance (Stanley 1979; Eldredge and Cracraft 1980; Vrba 1980; Paterson 1982a, 1986).

In terms of this model, Geocolaptes could be any age 'ancient' to recent. Just how old an 'ancient' living species is supposed to be has previously been a matter of guesswork. Authors who have used the term in this context have generally refrained from suggesting any time scale, although the implication in some cases is that species so labelled arose in some unspecified period prior to the Pleistocene. Estimates of the approximate age of a taxon can now be made from biochemical data, given certain presumptions in terms of the molecular clock theory. The assumed steady rate of molecular evolution has encouraged researchers to make statements about lineage lengths and about the time periods required for observed differences between taxa to have accumulated. Gillespie (1986) reveals, however, that the assumptions and models underpinning our understanding of molecular evolution are, at best, inadequate; the constancy of rate of molecular change is a matter of considerable debate (Hillis 1987), and Harrison (1989) points out that allele phylogenies are not equivalent to organism phylogenies. In fact, recent studies show that some alleles may be older than the species that carry them (Packer 1989). In any event, no biochemically derived estimate of the age of Geocolaptes has yet been published.

If the process of evolutionary change is pulsed rather than continuous then environmental forcing concomitant with climatic change is the likely agent. Our knowledge of past global climates is still imperfect but a review by Brain (1981) indicates 17 Pleistocene temperature oscillations with an approximate periodicity of 100 000 years. Such knowledge is far superior to that available to earlier researchers (e.g. Moreau 1966). A comprehensive and convincing account of the effect of the Pleistocene climatic history on the nature and diversity of the present-day African fauna and flora is provided by Kingdon (1989) and underlines the importance of this dynamic period.

An obstacle to the determination of the relationship of the African Ground Woodpecker to other African picids lies in the relative lack of biological information on all of these species. Although Eurasian and North American woodpeckers have been well studied, the same is not true for their African counterparts. Some indication of the poor state of knowledge can be gained from the recently revised Roberts' Birds of Southern Africa (Maclean 1985) in which the reader is refered to published references for only three of the seven species occuring in southern Africa and the Ground Woodpecker is not one of these three. In the definitive monograph Woodpeckers of the World (Short 1982), African woodpeckers take up less text than any other regional group with a mean of 2.1 pages per species. In contrast to this the woodpeckers of Eurasia and North America are accorded averages of 5.1 and 5.3 pages per species respectively.

A further difficulty of this study concerns the habitat and habits of the Ground Woodpecker itself. Although the birds can be picked out at a long distance, the rugged nature of much of the terrain they inhabit enables them to get out of sight very quickly when on the move, and a 30-second flight by a group of woodpeckers may result in an arduous hike of anything from forty minutes to two hours by the observer before contact can be re-established. Ground Woodpeckers are not easy birds to catch. In the

40-year history of bird ringing in southern Africa only four have been caught, two of these by myself in the course of this study. Roost holes are difficult to locate and often inaccessible; the birds do not voluntarily evacuate the holes on investigation and cannot be forcibly extracted from the offset sleeping chambers at the end of their one-metre-long tunnels. Given the difficulty of capture, colour-marking is seldom possible and in any event does not greatly facilitate individual recognition. Tarsal colour rings are not easily seen on the birds because of their habit of half squatting or lying on the rocks when 'perched'. Their plumage colouration and frequent bathing renders dye-marking ineffective except for periods of a few weeks. The possible use of other colour-marking tecniques (such as nasal saddles, streamers or collars) was not contemplated because of the unnatural mortality which can result from such devices as well as the potential increase of predation risk to the marked birds and also because of the possible modification of behaviour which such marking techniques might have induced (Burley et al. 1982, Hagen and Reed 1988). Futhermore, because so little was known of the behaviour of the species at the outset of the study, capture and marking procedures which might have caused the birds to forsake a particular roost site were avoided, especially since the location of a pair or group of resident Ground Woodpeckers in a logistically convenient area greatly facilitated behavioural observation and was too valuable to put at risk.

A technique that has facilitated study of other tunnel-nesting species such as bee-eaters (Meropidae) has been to dig trenches rearward of the bank face to permit access to the nest chambers (Fry 1985). This technique is impractical for the study of Ground Woodpeckers however, because of the usually steeply-sloping terrain, abundande of rocks and boulders and the shallow soils in which the birds often dig their tunnels.

The study of captive woodpeckers is a potentially rewarding technique (Kilham 1983; Sielmann 1959) but was

not an option in this part-time study which was constrained by limited funds and a full-time employment commitment.

I commenced this study knowing nothing at all about the Ground Woodpecker and my knowledge of the habits of woodpeckers in general was derived from casual encounters with four other species. I had no preconceived ideas about woodpecker relationships and, lacking familiarity with the family in general, I also lacked the basis on which to make intuitive predictions.

The main thrust of this study has been to get to know the Ground Woodpecker well enough in the field to be able to determine the nature of the character set that comprise its fertilization system, fit it for its normal habitat and dictate its ecology. These features of its biology and behaviour provide insight into its origin; into how its ancestors overcame the stress associated with an altered environment by efficient adaptation until their changed surroundings became normal to them. In the process, of course, they changed as well, so much so that, like Kipling's Armadilloes, they were quite different from what they had been before. These changes did not accumulate slowly over millions of years but evolved relatively rapidly in a small, isolated population. Such is the process of speciation as conceived here.

The recognition concept of species is followed in this study rather than the orthodox biological species concept (Dobzhansky 1937; Mayr 1942) because the latter concept places emphasis and reliance on ad hoc characters termed 'isolating mechanisms'. These characters are supposed to arise in diverging allopatric populations as a consequence of pleiotropy, but only become functional following range expansion and re-establishment of contact with the parental species, when the characters prevent interbreeding by the differentiated populations. There is ample evidence, however, (amongst land birds on oceanic islands, for example) that secondary overlap is not a prerequisite for speciation. As a consequence, the characters termed isolating mechanisms do not serve any isolating function and

should rather be labelled in accordance with their real functions, whatever they may be.

It is a common contention of opponents of Paterson's recognition concept that it is not basically different from the orthodox concept of Dobzhansky and Mayr but merely represents the 'other side of the same coin', to quote the popular metaphor. Those evolutionary biologists who find it difficult to regard the two concepts as mutually exclusive fail to distinguish between 'adaptations' which are fixed, species-wide characteristics, and those which are geographically and chronologically variable. A particular characteristic may be fixed and inflexible in some species but variable in others (clutch size in birds is an example); uncritical appraisal of species traits and muddling of adaptations with effects has great potential for misleading debate in evolutionary biology.

The primary merit of the recognition concept is that it allows one to visualize the speciation process taking place in the real world and to appreciate and understand the environmental stresses to which the animals had to adapt; species characteristics take on a new significance, challenging one to speculate on the circumstances that might have favoured their development. By contrast, for example, the hills and valleys of gene frequency in the theoretical landscape of genetic drift cannot be directly observed and must remain the abstract domain of the armchair theoretician.

As already stated, the Ground Woodpecker is a difficult species to capture and mark, and to keep under observation when the birds are on the move, especially in the southwestern Cape where I have resided for most of the study period. Consequently I have few data on group structure and reproductive behaviour. I have compensated for this in other aspects of the study, believing that "..research is surely the art of the soluble." (Medewar 1967).

The next five chapters present all that I have been able to learn from my own studies of the Ground Woodpecker and from the limited literature concerning it. Within

these data lie most of the threads of the Ground Woodpecker's history and some clues to its relationship. Chapter 7 explores the evidence for relationship and identifies an extant relative. Chapter 8 establishes the nature of the relationship and draws a plausible scenario of a sequence of events and conditions under which the Ground Woodpecker could have evolved. Finally, Chapter 9 provides a detailed hypothesis of the course of speciation in terms of Paterson's recognition concept of species, and explores the likelihood of the Ground Woodpecker having evolved in terms of the predictions of other concepts and modes of speciation.

o o o O o o o

2. DISTRIBUTION, HABITAT, TAXONOMY AND STUDY AREAS.

"One of the remarkable bird-products of South Africa; ....A woodpecker that has no interest in trees, but lives and gets its living on the ground.....Most often found on rocky hillsides, but sometimes in quite open country. Always fond of rocks, however, if any are to be had.

Leonard Gill (1936): A first guide to South African Birds.

DISTRIBUTION

The Ground Woodpecker is a southern African endemic. It does not occur north of the Tropic of Capricorn in any part of its range though it approaches this latitude (23°28'S) in the northeast; in the west of the subcontinent it is not known north of 28°S. Although such an extra-tropical distribution would automatically qualify it as a 'temperate' species in most terminologies, it is important to bear in mind that a climatic regime equivalent to that of the northern temperate zone does not occur south of the tropics in the southern continents (Darlington 1965).

The known distribution, based on recorded presence in one-quarter-degree (15' x 15') squares, is shown in Fig. 1. This is a 1987-1990 distribution, generated from records held by the Southern African Bird Atlas Project and is more comprehensive than that previously generated from regional atlasses, museum skins and literature records (Oatley 1989).

HABITAT

Rocks are common to nearly all areas inhabited by Ground Woodpeckers throughout their range. A profusion of blocks of stone littering sloping ground beneath an escarpment, mesa or butte is the type of area most commonly favoured by these birds. The only places in which they may be found far from rocky slopes are in eroded areas characterised by deeply incised dongas or dry gullies. Where rocks are not available or not big enough to provide

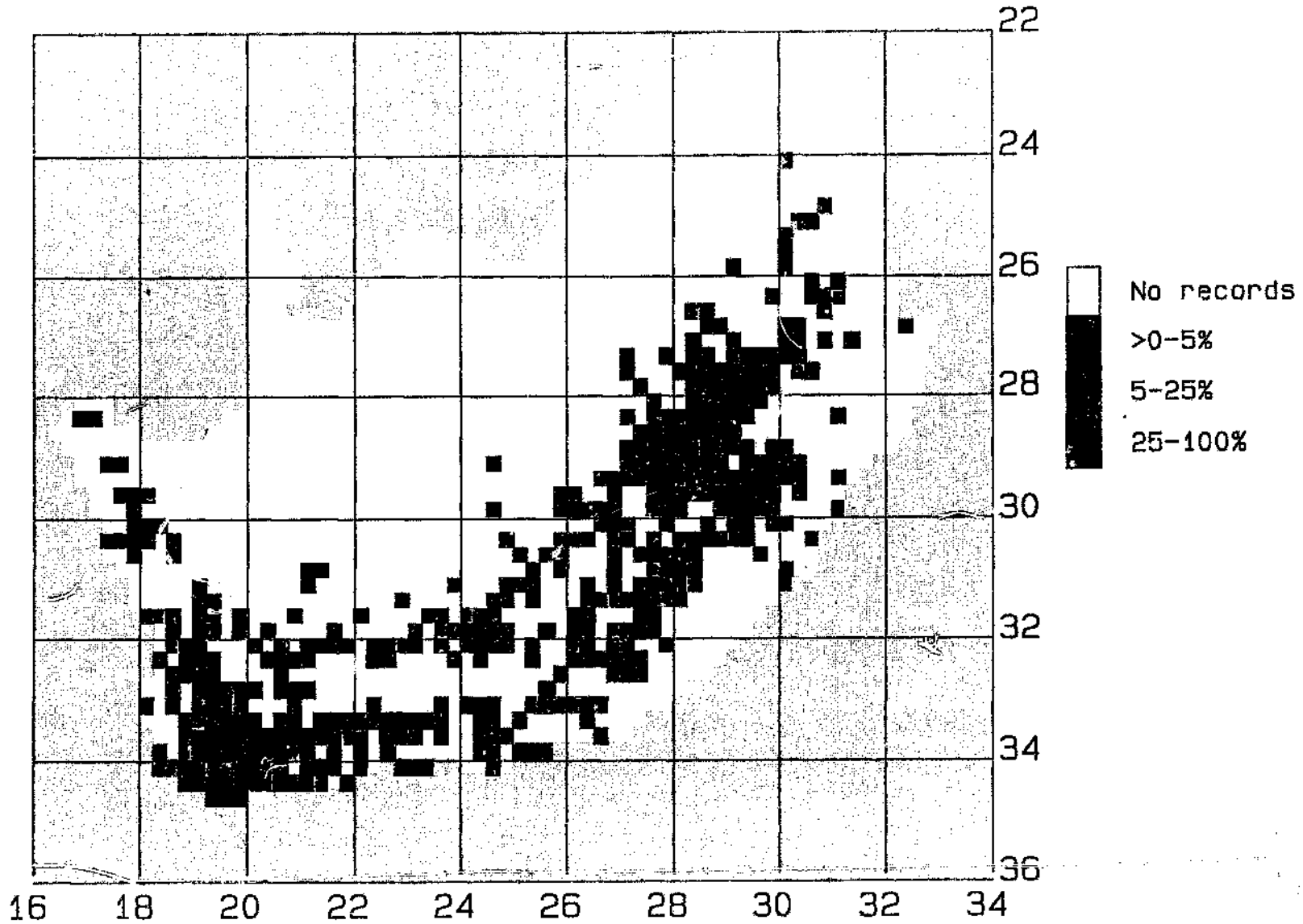

Figure 1. Distribution of the Ground Woodpecker. Shading percentages represent number of atlas cards per quarter degree square on which this species is recorded.

adequate vantage points, the woodpeckers perch on termite mounds, shrubs, trees, buildings or other man-made structures such as fences, telegraph poles or lines.

Because of the species distribution across nearly the full breadth of the subcontinent, the Ground Woodpecker's habitat cannot be defined in terms of any particular vegetation biome of the southern African region. In the broadest sense it can be said to be a non-forest bird, sensu Moreau (1966).

In the eastern part of its range it is found in the grassland biome of upland and montane areas of the summer rainfall region below about 2 865 m. In the alpine grassland above this level between the lip of the Drakensberg escarpment and the Lesotho watershed it occurs only as a summer breeding visitor (Brown and Barnes 1984). In this alpine zone, which averages 3 000 m altitude, July grass minima temperatures fall below -18°C and surface soil is regularly frozen and may remain so throughout winter on south-facing slopes (Edwards 1967).

In the southwest of its range the Ground Woodpecker lives throughout the winter rainfall area in the fynbos biome occurring at all levels from the mountain heights to the seashores where its foraging sorties on boulder beaches extend into the splash zone of high spring tides. Rocky habitats abound in this region, but the Ground Woodpecker is not common.

The northwest of the species range lies in the Springbok - Steinkopf area of Namaqualand. In this arid region the drought-resistant vegetation has affinities with the Paleotropical floral Kingdom and the annual precipitation is approximately 220 mm on average with about three quarters of this falling in the winter months April to September. The hot, dry summers shrivel up annual plants and produce a stark landscape with very high ground temperatures and no shade-providing trees.

In broad terms habitat must provide food, shelter and breeding sites. As will be shown in ensuing chapters, the Ground Woodpecker eats only ants and bores tunnels in vertical soil surfaces for purposes of roosting and breed-

ing. Ants are generally everywhere available, especially in surface soil, and there are few terrestrial environments in which potential tunneling sites in soil banks could not be found. Neither of these two essential components of habitat is therefore likely to be limiting. Vegetation can be a constraint when it becomes too dense, covers all open ground, and restricts visibility. For example, fynbos vegetation of the winter rainfall area varies in composition, height and density depending on fire frequency. Large tracts of barren, ash-covered hillside such as occur and persist for several months after fire are not frequented by Ground Woodpeckers, probably because there is insufficient shelter from avian predators. The other extreme of fynbos succession is also unsuitable because vegetation overgrows footpaths and other feeding sites and restricts the visibility needed for early detection of predator approach. Optimum conditions for Ground Woodpeckers lie somewhere between fire and climax; experience at Elsies Peak study site (page 16) indicates that the habitable stage of fynbos succession may last for only three to four years. This factor is probably partially responsible for the relative paucity of the species in the southwestern Cape, the other factor being the hot dry summers. Ground Woodpeckers are easily heat-stressed and need water to drink and bathe in when diurnal temperatures are high (Chapter 3). Total absence of surface water in any area will therefore preclude habitation by Ground Woodpeckers and the need to minimize evaporative water loss confines them to high ground (where temperatures are lower) in arid regions. This is nowhere better demonstrated than in the Great Karoo where Ground Woodpeckers avoid the central basin but occur on the high ground around its perimeter (Fig. 1).

TAXONOMY

Geocolaptes olivaceus was first described under the name Picus olivaceus by Gmelin in 1788 from the type locality "Cape of Good Hope". In 1831 Swainson placed it in its present monotypic genus Geocolaptes. It has subse-

quently been subdivided into geographical races, though it is noteworthy that 161 years passed before the first such race was described by Meinertzhagen (1949) who gave the name theresae to populations in what was then called Little Namaqualand. The description was based on two specimens collected north of Springbok.

Clancey (1952; 1957) subsequently recognised as many as five geographical races. Within ten years this array had been reduced to three races (S.A.O.S. List Committee 1969). Short (1982) recognises only two subspecies, the nominate one being from the western and central Cape Province and G. o. prometheus Clancey for all populations eastwards. In a reappraisal of the so-called subspecific variation in this species, Earlé (1986) demonstrates convincingly that the characters used by Clancey (1952) to subdivide the populations are not geographically localised and are manifested by individuals throughout the species range. Earlé accordingly proposes that G. o. prometheus and G. o. petrobates are synonyms of G. O. olivaceus, thus restoring the status of Geocolaptes olivaceus as a monotypic species.

Birds in Natal and the Orange Free State do appear paler than those in the southwestern Cape Province but Earlé (op. cit.) shows that this variation is clinal. I know of no behavioural differences between birds of any two areas, even between western and eastern extremes of range. There are thus no compelling grounds for according racial status to any arbitrary subsample of the population.

STUDY AREAS.

Areas in which Ground Woodpeckers have been studied in the course of this research can conveniently be grouped into three categories: the main study sites, secondary sites (those to which two or more visits were made) and single visit sites which were visited once only for periods ranging from a few hours to a few days.

Main study sites:

1. Wellington Farm, Tweedie, Lions River district, Natal;

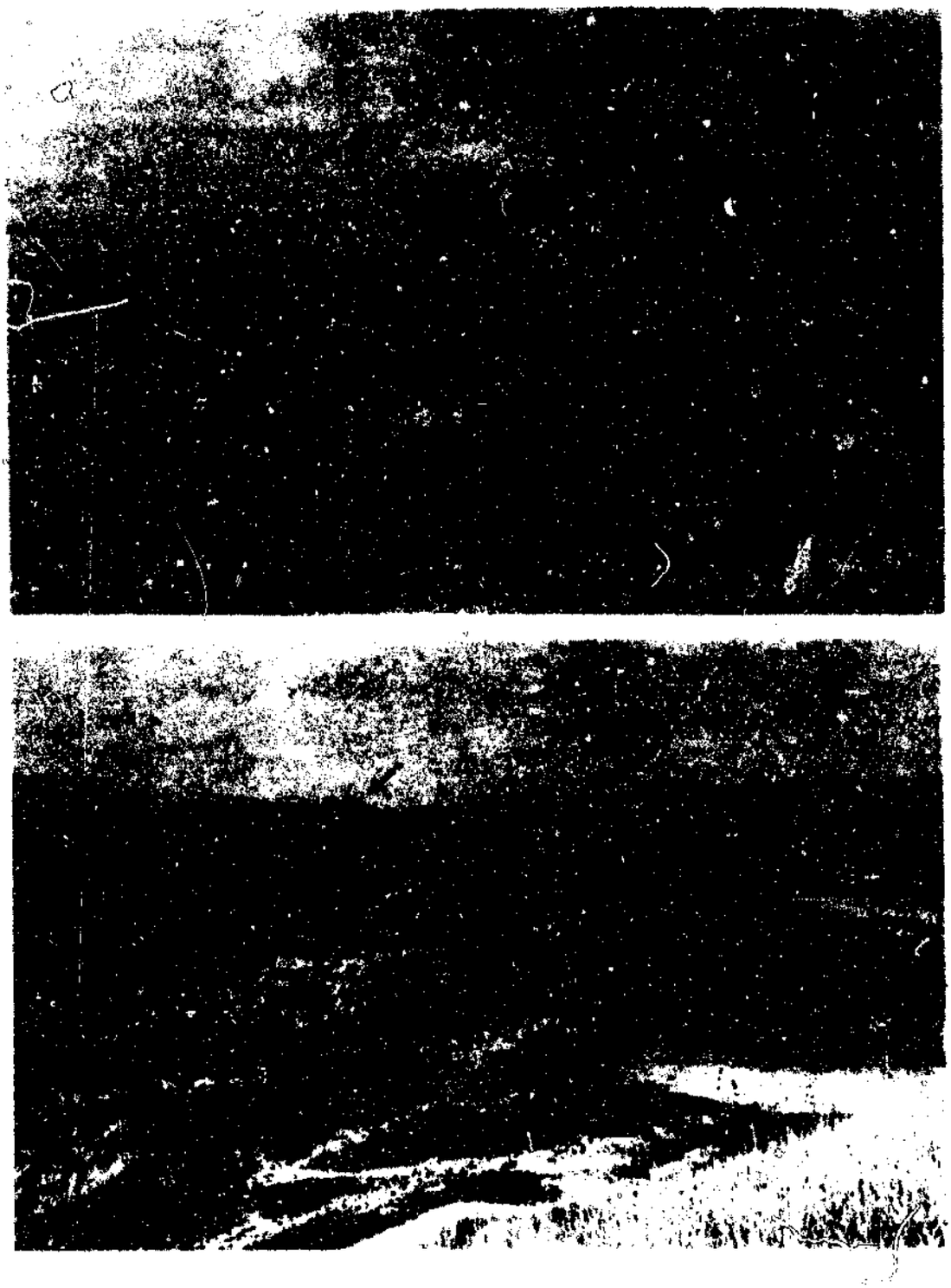

Figure 2. The Wellington study site showing (top) the grass-covered valley sides and one rocky ridge, and (bottom) the dam; the roost tunnels are in the shadowed bank and a favoured rock, on which the woodpeckers regularly rested, is arrowed.



Figure 3. The Glencairn Valley, Cape Peninsula. Elsies Peak is to the right, out of the picture. Ground Woodpeckers regularly foraged on standing dead wood in the vlei (centre right) and on the firebreak behind the houses (left of centre).

29°27'S, 30°11'E. January - November 1980, June 1985, June 1986. A steep-sided valley at 1 200 m altitude of open sour grassveld with rocky ridges. A deeply incised rill fed a small farm dam, the cut-away bank at one side of which contained several holes used by the Ground Woodpeckers (Fig. 2).

2. Elsies Peak, Cape peninsula, southwestern Cape Province; 34°09'S, 18°26'E. Elsies Peak is the highest point of a mountain ridge running westwards from the False Bay coast between Fish Hoek and Glencairn. The study area includes the upper slopes of the ridge and the Glencairn valley, where the author has resided since 1981. The vegetation of the upper ridge is montane fynbos; the valley is characterised by a vlei (a reedy marsh) with extensive stands of Typha and wind-sheared patches of alien Acacia cyclops (Fig. 3). I first observed Ground Woodpeckers in Glencairn in October 1982; observations on the peak ridge were commenced on a regular basis in February 1984. The altitude ranges from sealevel to 280 m on the ridge.

Secondary study sites:

3. Carlisle Farm, Dargle, Lions River district, Natal; 29°24'S, 30°04'E. Observations were concentrated on the escarpment ridge at 1 392 m and the rock strewn slopes falling away to the northwest in grazed sour grassveld. The majority of observations were made during six visits between July and November 1979.

4. Castledene Farm, Underberg district, Natal; 29°48'S, 29° 16'E. The farm lies astride the north-south aligned Mzimuti valley in the Drakensberg foothills. Observations were made on the western side of the valley on the slopes of Bucquay Peak between 1 700 m and 1 950 m (Fig. 4). Short grassveld with steeply graded and deeply incised drainage lines with permanent water. Observations were made during five visits between May 1979 and July 1985.

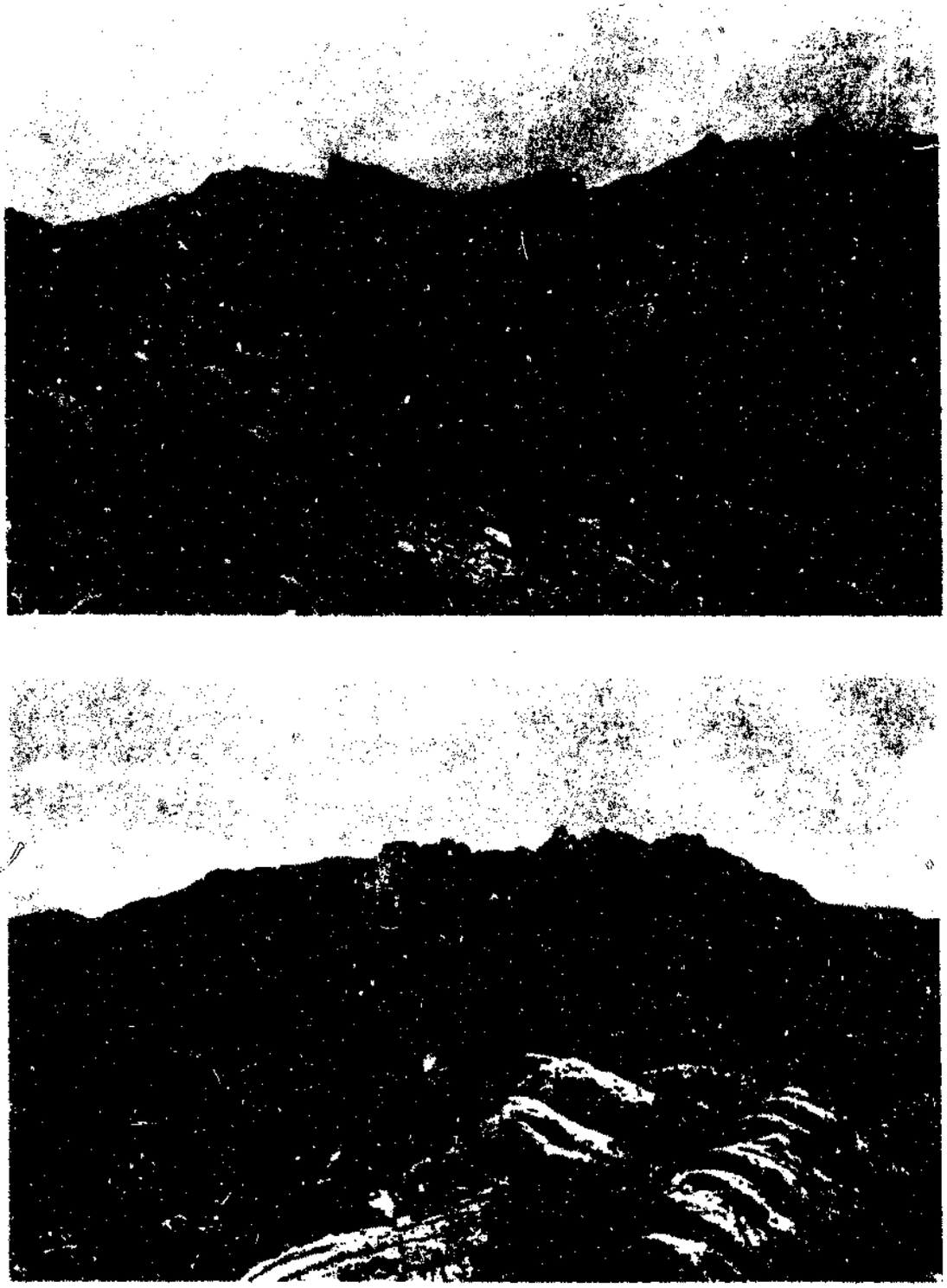

Figure 4. Rock-strewn slopes of Bucquay peak, Castledene, looking north towards main Drakensberg escarpment (top) and east across Mzimuti valley to Gardens Castle ridge (bottom).

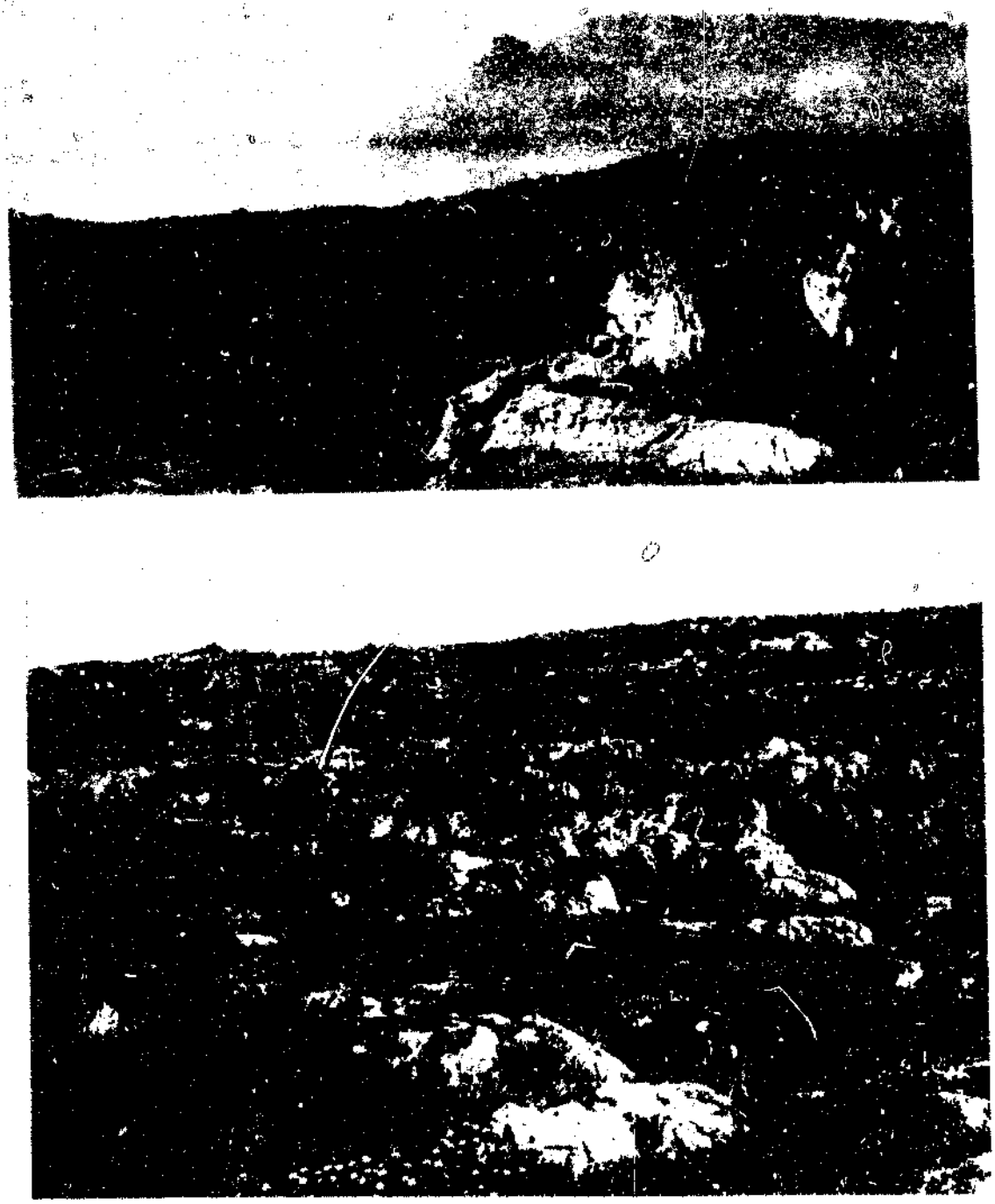

Figure 5. Slangkop study site on Atlantic coast of Cape peninsula. The view north towards Chapman's Peak (top), and general aspect of the Ground Woodpeckers' favoured foraging area (bottom).

5. Slangkop, Cape peninsula; 34°09S, 18°20'E; Montane fynbos at 100 - 120 m altitude on the western side of the peninsula (Fig. 5). Twentytwo visits were made between May 1981 and October 1982.

6. Coleford Nature Reserve, Underberg district, Natal; 29°56'S, 29°26'E. A steep grassy valley with a perennial stream. Study visits were made in December 1979 and June 1980. Mean altitude is 1 650 m.

Single visit sites:

7. Kamberg Nature Reserve, Estcourt district, Natal; 29°-24'S, 29°42'E. Observations on mountain slopes above Stillerust at 1 800 m altitude, September 1979.

8. Solitude, Giant's Castle Game Reserve, Estcourt district, Natal; 29°12'S, 29°26'E. Observations on three days in July 1980.

9. Cedarberg Mountains, Clanwilliam district, western Cape Province; 32°22'S 19°07E. Observations made during a two day hike through the Middelberg - Crystal Pools - Shadow Peak area, 1 000 - 1 500 m, in November 1982.

10. Sir Lowry's Pass, Somerset West district, southwestern Cape Province; 34°09'S, 18°56'E; summit ar ., 500 m altitude. August 1984.

11 Wonderkop, Ladybrand district, Orange Free State; 29°-04'S, 27°30'E; 1 500 m altitude. Short grassveld dotted with mounds of harvester termite Trinervitermes sp. Some donga erosion but no rocks apart from a pile of roadside boulders where the Ground Woodpeckers frequently perched. August 1985.

12 Golden Gate Highlands National Park, Clarens district, Orange Free State; 28°30'S, 28°37'E; 2 000 m altitude. Grassy valleys with deeply incised drainage lines between sandstone-capped ridges. August 1985.

13. Korannaberg, Winburg district, Orange Free State; 28° 25'S, 27°13'E; a large mesa rising 300 m above the surrounding plain to 1 800 m. Extensive deep donga system at foot of mesa on the farm Magerman's Hoek. August 1985.

o o o O o o o

3. DIURNAL ACTIVITY AND BEHAVIOURAL THERMOREGULATION

"The drummers of the bird world wake comparatively late, which is quite understandable since they sleep in holes in the trunks of trees (except in the incubating period) and are only roused by the growing light outside."

Heinz Sielmann (1959): My year with the woodpeckers.

INTRODUCTION

It is a commonplace observation that Ground Woodpeckers do not appear to do anything. In contrast to the restless activity of most small to medium-sized birds, the long periods of inactivity which seem characteristic of the Ground Woodpecker both impress and disappoint the casual observer.

Inasmuch as every bird must devote a certain proportion of its waking hours to seeking and consuming food, any remaining portion of its time is available for other activities. In broad terms therefore, the bird's day is divisible into foraging and non-foraging periods. The scale of this division has far-reaching effects on the species' life history.

Early research in this project was devoted to the study and quantification of the daily activities of a pair of Ground Woodpeckers on the farm Wellington.

METHODS

The study site comprised the two sides and floor of a narrow valley in grass-covered hills (Fig. 2, p.16) which made up the home range of a pair of Ground Woodpeckers. The birds were first discovered at the site in January 1980. Quantified observations were commenced on 23 March 1980 and continued until 30 November of the same year.

The first task preceding any observation period was to locate one or both woodpeckers (they were usually together). Once this was achieved I would move into a

position on the hillside directly opposite to their position and sit down. The birds were kept under observation with x9 magnification binoculars and continuous voice commentary on their activities was recorded with a tape recorder. Commentary periods were initially limited to ten minutes duration and although some were shortened because the birds moved out of sight, it quickly became evident that arbitrary curtailment of observation periods tended to result in the non-recording of change-over in the pattern of activity. Subsequent commentary periods were continued until both birds had left the field of observation or until the tape ran out.

All taped commentaries were subsequently transcribed into codes and entered onto sheets with each row representing one minute of real time. Physical parameters coded for each minute period included weather, air temperature, wind strength (Beaufort scale), wind direction and the aspect of the birds' location. In addition to actual activities (including vocalizations, displays and comfort movements), perching orientation, posture and activity substrate was recorded for each bird.

This observation technique was used in some other Natal study sites (Solitude and Coleford) for larger groups of woodpeckers.

Air temperatures were recorded for the majority of observation periods with the aid of a maximum-minimum thermometer placed on the ground next to me and, when necessary, in my shade. This appeared to be the best means of approximating the ambient temperatures experienced by the birds.

RESULTS

A total of 3 186 bird-minutes of observation were accumulated (one bird minute represents the activities of one woodpecker recorded for one minute). The bulk of these (2 774) were from Wellington and provide the basis for the quantitative data that follow.

Daily activity pattern.

Ground Woodpeckers emerge from their holes at first light, usually when it is barely light enough for a human observer clearly to discern movement. It is usual for all members of a group to share a single roost hole and individuals emerge in fairly quick succession. Before establishing this early departure I had expected that the woodpeckers would be late emergents and not leave the burrow until there was strong daylight. This expectation was based on the reasoning that the darkness of the roosting chamber would not be ameliorated until the exterior light intensity was sufficient to penetrate the length of a one-metre-long tunnel. Sielmann (1959) comments on the late rising of European woodpeckers and similar behaviour is shown by at least two African species, the Knysna Woodpecker Campethera notata and the Olive Woodpecker Mesopicos griseocephalus (pers. obs.). Ground Woodpeckers, however, appear not to rely on light increase or the early morning calls of other birds to wake them up.

On 26 July 1980 the two Wellington woodpeckers were caught in a mistnet late one afternoon and held overnight in a shoebox in which a layer of dry soil had been placed. Aside from some exploratory tappings on the walls of this artificial chamber, they seemed to settle down quite well. Fully thirty minutes before first light however, whilst the room and the interior of the box was in complete darkness, the birds became very active, shuffling around and raining blows on the sides of the box. This indicated a well-developed internal 24-hour rhythm and showed that the birds were not using light intensity or other external cues for initiating daily activity.

Having emerged from their hole the woodpeckers fly to a favourite perch (usually a large rock) where they may sit for some ten minutes before flying off to start foraging. Active feeding behaviour may take place at any time throughout the day and though weather conditions obviously can affect the duration and frequency of foraging and non-foraging periods, the latter predominate in

the forenoon and early afternoon and are devoted to 'resting'. At such times the birds are usually to be found perched on a large rock, facing into the sun and moving very little. Resting periods frequently last for 30 to 40 minutes. The longest period recorded involved a group of six birds at Elsies Peak and lasted 72 minutes from when observation commenced until the birds moved off to feed. The period was possibly much longer since the birds were well settled when first observed.

Inclement weather often causes the birds to seek shelter under a rock or in a hollow or overhang in an earthen bank. Shelter from high winds is achieved by perching on the lee side of a rock (or roofridge of a building). Cold bleak conditions may result in the woodpeckers going to roost 30 to 45 minutes earlier than they would do in fine weather, when the burrow is entered virtually at dusk. In general this species seems much more susceptible to heat stress than to cold. In hot weather the birds actively seek shaded rocks for rest periods and frequently resort to bathing. On such days drinking occurs, particularly before going to roost.

Proportion of time spent foraging.

The overall total of 3 164 bird-minutes of observation included 857 minutes of foraging, or 26.9% of the total period. This total, however, includes observations of different groups of woodpeckers in different areas. A more realistic figure is obtained if the data are restricted to the Wellington birds for the six months April to September. These include the coolest and driest months of the year when insects are theoretically likely to be lowest in numbers and therefore less available as a food resource for insectivorous birds. At the latitude of Wellington the mean daylength for the six months is very close to twelve hours. Ambient temperatures recorded during observation periods ranged from 2° to 30°C; the overall mean temperature of observation periods for April to September was 16.7°C. The total bird-minutes recorded for these six months were 2 455 of which 755, or 30.8% involved foraging

behaviour. However, the distribution of observation periods with respect to diurnal hour periods is uneven because birds could not always be located. Only two observation periods were recorded between 06h00 and 07h00, and both of these were of birds leaving the roosting burrow; they could not easily be relocated after they had flown off, presumably to forage. Because of this, these records do not reflect the proportionate amount of foraging which might be expected to occur in this early period. The totals of observation minutes and foraging minutes recorded for each hour period are shown in Table 1.

If it is assumed that the observed ratio of foraging to total minutes of observation for each hour is a reasonable reflection of the true foraging rate for that hour, then it is possible to estimate the number of foraging minutes that would be recorded if the observations were equably distributed throughout the daylight period. By further assuming that the foraging rate for the first hour of the day is equal to or not less than that for the last hour, the figures can be extrapolated to cover a twelve-hour day. Table 2 gives the estimated figures and the percentage of each hour devoted to foraging. These add up to 238,9 minutes, 33.2% of the 720 available minutes of daylight. Fig. 6 portrays in diagrammatic form the estimated percentage of each daylight hour which the woodpeckers devote to seeking food.

On the basis of these figures it seems reasonable to conclude that Ground Woodpeckers are able to find and consume their daily food requirements in about one third of the daylight hours during the cooler half of the year. Details of feeding technique and diet are presented in Chapter 4.

Perching, preening and comfort movements.

The word 'perch', employed either as a noun or a verb, commonly connotes a twig or branch or the use thereof, and is therefore inappropriate for Ground Woodpeckers whose preferred perch is always a rock. There is no suitable

TABLE 1. Total minutes of observation on, and of observed foraging by Ground Woodpeckers at Wellington, April to September 1980.

Hour commencing	06h00	07h00	08h00	09h00	10h00	11h00
Minutes spent foraging	-	24	82	87	91	35
Total minutes of observation	-	58	186	181	302	257
Hour commencing	**12h00**	**13h00**	**14h00**	**15h00**	**16h00**	**17h00**
Minutes spent foraging	46	34	84	82	109	79
Total minutes of observation	285	149	334	253	257	193

TABLE 2. Estimated number of minutes spent foraging in each hour, and percentage of available time used by Wellington Woodpeckers.

Hour commencing	06h00	07h00	08h00	09h00	10h00	11h00
Estimated No. of minutes foraging	24.6	24.8	26.5	28.8	18.1	8.2
Percentage of available time	40.9	41.4	44.1	48.1	30.1	13.6
Hour commencing	**12h00**	**13h00**	**14h00**	**15h00**	**16h00**	**17h00**
Estimated No. of minutes foraging	9.7	13.7	15.1	19.4	25.4	24.6
Percentage of available time	16.1	22.8	25.1	32.4	42.4	40.9

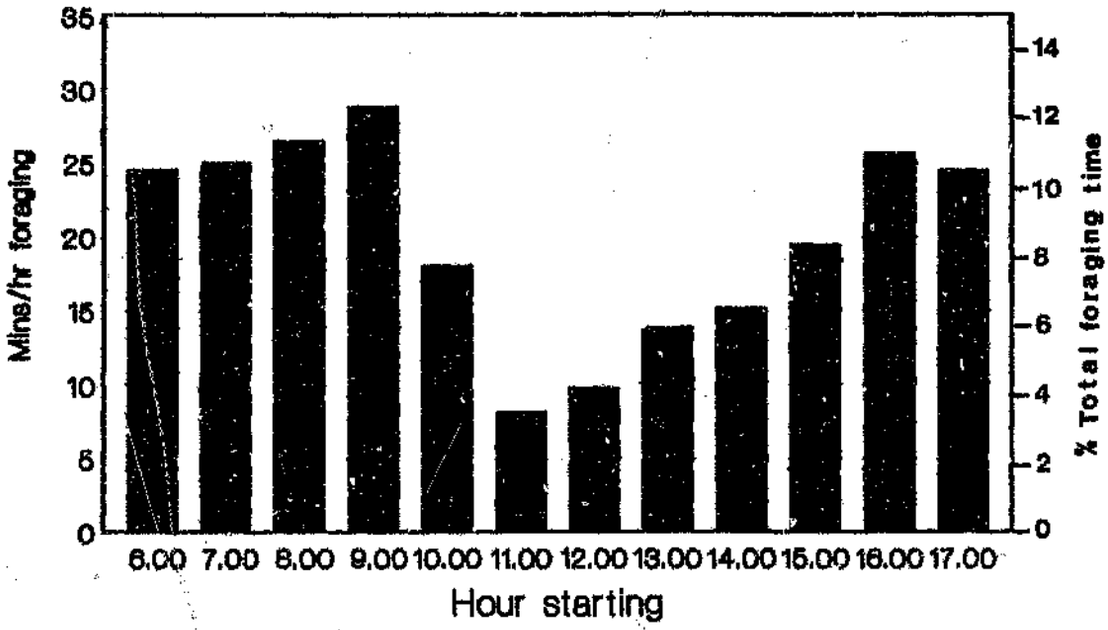

Figure 6. Estimated daily distribution of foraging activity by Ground Woodpeckers at Wellington for the months April to September; bars represent minutes per hour on the left scale (solid lines) or percentage of total daily foraging time on the right scale (dashed lines).

synonym for the word, however, and 'perch' is used hereafter to describe either "an elevated position" (as defined by the Oxford English Dictionary) or the stance taken by a woodpecker on any elevated substrate.

Prolonged perching is practised by Ground Woodpeckers in two sets of circumstances for quite different reasons. In the first instance, it is characteristic of resting birds and in such cases all members of the group will usually be found on the same rock (or, occasionally, tree or roofridge) in relatively close proximity to each other. Such birds appear to be relaxed (though they are always looking about) and they usually adopt a half-squat, resting on their tarsi. Sometimes a full squat position is adopted in which the bird rests its belly on the substrate. Preening often takes place and comfort movements such as wing-stretching and wing-raising also occur.

Perching for a quite different purpose results when a group is actively foraging and involves a solitary bird acting as a sentinel. This bird seeks an elevated position in the immediate vicinity of the foraging group; if a rock is not available it will use any substitute from a bush or tree to a pole or fence wire. Such sentry birds seem seldom to have to stand duty for more than ten minutes or so before being relieved by the mate (when only a pair are involved) or another member of the group. The relieving bird usually wipes its beak on the lookout substrate and the two may sit together for a minute before the original sentry drops down to the ground to forage. This aspect of Ground Woodpecker behaviour is discussed further under the heading 'Predator avoidance behaviour' (Chapter 5). The phenomenom of sentinel birds needs to be kept in mind in any consideration of the diurnal distribution of perching inactivity by Ground Woodpeckers.

In the case of the Wellington pair, both birds foraged simultaneously in the early morning and late afternoon when the motivation to feed was probably strongest. During the breeding season the mate of an incubating bird must also forage without the safeguard of a lookout bird. In groups, particularly of four or more birds, there seems

always to be sentinel, even in the most intensive foraging periods. Theoretically, where groups of three or more birds are present, apparently 'inactive' birds can be expected throughout the daylight hours.

Preening is performed during such periods, both by resting birds and, on occasion, by sentinel birds. A total of 10,8% of all quantified perched time was devoted to preening. When two or more birds are resting in close proximity, initiation of preening activity by one bird frequently results in similar behaviour by the other bird or birds in the group. Allopreening has not been observed at any time. Head-scratching occurs regularly, not always in association with preening. Like other woodpeckers and most non-passerines, Ground Woodpeckers employ the direct method of head-scratching (Simmons 1957, Nice and Schutz 1959, Burtt and Hailman 1978).

Various other comfort movements are frequently performed. The commonest, which usually follows long periods of inactive resting, is the wing-stretch - wing-raise sequence. In this movement, one wing is extended horizontally outwards and backwards whilst the leg on the same side is also extended out sideways and rearwards. This is usually followed by the simultaneous raising of both wings in the flexed position vertically above the back.

Perching orientation.

It soon became evident that Ground Woodpeckers perched facing the sun, a pattern I call sungazing. When quantification of observation periods started, the perching orientation was one of the variables noted from the outset. Birds were scored as either facing the sun or perched at approximate angles of 45°, 90°, 135°, or 180° (back to sun).

The results show convincingly that in conditions of direct sunlight perched birds orientate toward the sun in the great majority (82,9%) of occasions (Fig. 7a). Under conditions of obscured sun (because of cloud or land shadow) orientation is diverse (Fig. 7b). The fact that a significant proportion (almost 43%) of birds perched at an

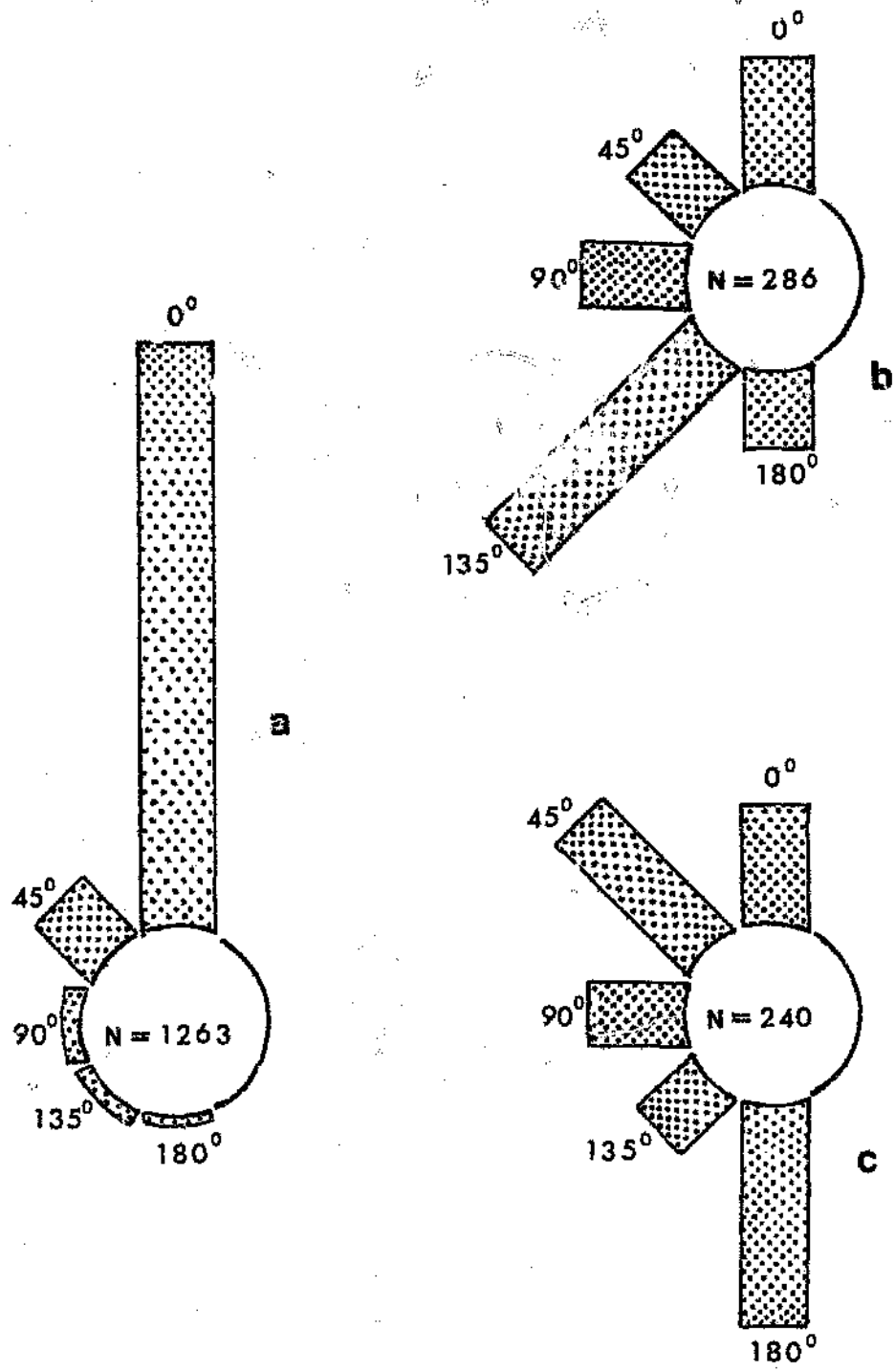

Figure 7. Perching orientation of Ground Woodpeckers at Wellington with respect to (a) visible sun; (b) obscured sun; (c) wind direction when sun obscured. Birds orienting to 0° are facing into sun or wind. Sample sizes represent bird-minutes of observation.

approximate angle of 135° to the hidden sun was partly due to the north-south alignment of the valley which meant that in many early morning and afternoon observation periods the sun was hidden by ridges and under conditions of land shadow the perched birds preferred to face down the valley, rather than into the hillside; this usually resulted in a 135° angle to the sun position. There is also the possibility that the woodpeckers were orienting to wind. Fig. 7c shows the proportions of orientation at different angles to the wind under conditions of no direct sunlight. Table 3 gives the figures for all 'no sun' orientations and the resultant angles of perched birds to whatever wind was prevalent at the time. There were 46 cases (bird-minutes) in which there was no wind at all. For the balance, most sat with their backs to the wind. It was not noted, however, how sheltered were the actual positions on which the woodpeckers were sitting because this was not always easy or even possible to assess from a distant point. Ground Woodpeckers are, however, tolerant of wind on their backs, even when it is strong enough to lift the feathers of their mantles.

In general, the urge to face the sun seems greater than any other consideration. In June 1981 a group of three Ground Woodpeckers were watched sitting on a flat-topped rock pinnacle at the Slangkop study site. The rock was in the shadow of the cliff and the birds were facing west, out to sea. When, after ten minutes, sunlight came to bear on the rock, all three woodpeckers turned very deliberately to face northwards along the cliff face, directly into the sun. There was no immediate change in temperature and there was no sign of raised or sleeked plumage before or after the event to indicate that the birds were actively adjusting the insulating effect of their feathers in response to a temperature change.

Fluffed plumage (partial erection of body feathers to trap air and improve insulation) is not commonly observed in Ground Woodpeckers. In the course of the Natal observations it occured in only 82 of the 1 637 bird-minutes during which plumage condition was noted, or 5% of the

TABLE 3. Perching orientation of Ground Woodpeckers to wind direction in absence of direct sunlight.

Approximate angle to wind	Angle of orientation to obscured sun					TOTAL
	0°	45°	90°	135°	180°	
0°	6	5	7	23	0	41
45°	19	9	23	9	4	64
90°	10	13	1	4	4	32
135°	2	0	5	6	14	27
180°	3	2	4	67	0	76
TOTALS	40	29	40	109	22	240
NO WIND	16	8	2	13	7	46
GRAND TOTALS	56	37	42	122	29	286



Figure 8. A shaded rock, favoured as a midday resting site in hot weather by Ground Woodpeckers at Castledene.

time. Sixtynine of the 82 minutes were in conditions of no sun, but in 275 minutes of similar conditions the birds displayed normal plumage posture. The minimum, mean and maximum temperatures measured in conjunction with fluffed and normal plumage states under sunless conditions (land shadow or overcast) were 2 - 8,9 - 26°C and 2 - 15,5 - 25°C respectively. Fluffed plumage on birds perched in direct sunlight was only observed on one occasion for a period of 13 minutes. The ambient temperature at the time was 15°C.

Orientation toward the sun has been shown to be a form of behavioural thermoregulation in the Herring Gull Larus argentatus to minimise heat gain under conditions of thermal stress (Lustick et al. 1978). Herring Gulls have light ventral plumage and dark dorsal coloration. There is thus a sharp contrast between upper and lower surfaces, a feature which the Ground Woodpecker does not have. However, by facing the sun the minimum body surface is exposed to direct and reflected solar radiation.

Several features of Ground Woodpecker behaviour suggest that they are more easily stressed by heat than by cold. In hot weather they forsake favourite perching positions and seek shaded perches, either on the southern side of the same rock or in the shade provided by trees, especially those growing in rock clefts (Fig. 8). They bathe in the hottest parts of the day and drink before going to roost on hot days. The most dramatic demonstration of their relative susceptibility to heat stress that I have witnessed occured at Wellington when, at about midday, the two woodpeckers were perched on the obverse face of a large rock, facing the sun and gaping with very sleeked plumage postures. At the same time and for several minutes, a male Buffstreaked Chat Myrmecocichla bifasciata was perched within a half-metre of the woodpeckers on the same rock but on the hotter incident face of the boulder, and showing no signs of heat stress whatsoever. At 125 g the Ground Woodpecker has more than three-and-a-half times the mass of the 34 g Buffstreaked Chat and should theoretically be able to endure a greater heat load than the

smaller bird.

When perched facing the sun, woodpeckers usually choose to stand or squat on the obverse face rather than the face incident to direct sunlight (552 recorded instances of use of obverse side; 31 instances of perching on the incident side). The favoured resting posture of the Ground Woodpecker is one in which it rests on the length of its tarsi (termed 'half-squat' in this study). Alternative postures are 'standing' (occasionally on one leg) and 'full squat' in which the bird rests its belly on the perch substrate. In a total of 1 707 bird-minutes in which postures were recorded, half-squat occured in 1 187 (69,5%), standing in 487 (28,5%) and full squat in 33 (1,9%). Although it seems obvious that the half-squat position is the most natural for a woodpecker (it is the horizontal equivalent of the 'propped' position adopted on a vertical trunk by an arboreal woodpecker) it is possible that its employment in conjunction with a cool substrate (such as an obverse rock face) could serve a thermoregulatory function.

o o o O o o o

4. DIET AND FEEDING HABITS

"During winter the nests of Formica rufa L. often show the following features: holes with a diameter of 5-10 cm, and a depth of 10-50 or sometimes even 100 cm, and characteristic animal droppings which resemble burned cigarettes and which contain many remnants of ants.
What sort of animal is the delinquent here and what is the influence of this house-breaking and mass-murder on the survival of an ant nest?"

Gerrit J. De Bruyn et al. (1972): Predation of ants by Woodpeckers.

INTRODUCTION

Published references indicate that the Ground Woodpecker eats mainly ants, or ants and other insects. Short (1971d) states that he found only ants in the stomachs of birds collected. Labels of museum specimens list ants, ants and grubs, or insects, but such descriptions are possibly as indicative of the collector's ability to identify invertebrates as they are of the bird's food. Inasmuch as ants are insects and the whitish pupae and callows could well be described as grubs, such descriptions do not necessarily indicate that insects other than ants are eaten.

The diet of the Ground Woodpecker has been extensively investigated in this study and the species is revealed as highly specialized, both in its food and in the manner in which it obtains it.

METHODS

Diet has been determined mostly from the microscopic examination of faecal samples. The Ground Woodpecker voids relatively large and distinctively-shaped faecal pellets which, in fine weather, dry out in the course of a few hours and accumulate on and around boulders favoured as

resting perches. Because of their size and shape these faecal pellets are not easily confused with those of other birds which may perch on the same rocks.

Samples collected at such sites were stored dry in bottles labelled with the locality and date. Examination was conducted under a x10 binocular microscope. A portion of the sample, equivalent in volume to about half of an average-sized faecal pellet, was placed in clean water in a circular plastic container 70 mm in diameter. The base of the container was marked off in three concentric circles and four quadrants, each quadrant boundary demarcated in a different colour. Once the faeces sample had softened in the water it was broken up with forceps and then agitated to spread the material evenly over the surface of the container. The container was then rotated anti-clockwise under the microscope and the markings facilitated orderly scanning of the material.

An analysis sheet was drawn up for each sample, site, and date; the number of subsamples was scored along with each identifiable genus of ant and the presence of ant brood (eggs, pupae and cocoons), alates and imagos. Other material was also scored for each subsample when present. Insect remains in Ground Woodpecker faeces are very fragmented, far more so than is the case in the faeces of much smaller insectivorous birds such as robins (Oatley 1970). Thoracic segments, head capsules and, in some instances mandibles, are distinctive and enable identification of ants at the generic level. Ants which were intact or only partly dismembered were removed from the samples and stored in alcohol; species identification was frequently possible from these specimens.

Collection of faecal samples was opportunistic in seldom visited localities but in two study areas (Elsies Peak and Golden Gate Highlands National Park) was regularly undertaken to provide a monthly record of diet for periods of at least one year.

The advantage of studying a bird with so restricted a diet is that the investigator can quickly become familiar with the prey species and is not faced with the bewilder-

ing variety of invertebrates which more generalist insectivorous birds in Africa are apt to eat. Collections of ants were made in various study areas and submitted to Dr. A.J. Prins of the South African Museum for specific identifications. These specimens formed a named collection with which the fragmented portions of ants found in faecal samples could be matched. Ants collected in the field were placed into a bottle containing clean water and a wetting agent. Specimens were subsequently sorted into species and stored in 70% alcohol in dental anaesthetic tubes.

Three random ant sampling techniques were employed in the field. The first, a modified line transect technique, was designed to provide a comparative measure of ant availability within and outside of areas occupied by Ground Woodpeckers. A random bearing was taken and at every third pace the ground within arms reach was closely scrutinised for ant nest entrance holes. Two such holes (or, in the absence of holes, other likely ant nest sites) would be sampled by striking a knife blade to an approximate depth of 5 cm and then turning up the surrounding soil. The strike was recorded as positive or negative depending on the presence or absence of ants in the turned-up soil. If termites were found instead of ants the strike was scored as negative but annotated with a 'T'. A total of fifty sampling points (with two strikes at each) were scored to give a transect length of approximately 150 m. If a sampling point fell on outcropping rock or on a boulder, strikes would be made in the nearest soil at right angles to the sampling point. This technique yielded a comparative measure of ant availability in the soil substrate and also provided a conservative measure of the abundance of termites, relative to ants, in the area.

The second ant sampling technique involved walking through the study area, usually on a circular route, and collecting single individuals of ants encountered on the surface of the ground or on rocks or plants. These ants were subsequently sorted into genera and counted. This provided a measure of abundance of different genera and their representation in these samples could be compared

directly with their frequency of occurrence in Ground Woodpecker faecal samples from the same area.

The third technique involved a random search for ants' nests under stones. The stones had to be of a size such that a Ground Woodpecker could reach with its tongue any ant brood deposited against the undersides, and sufficiently free of vegetation to permit exposure to sunlight and close approach by the bird. All stones investigated were inverted and scored for one of three categories: 'no ants', 'ants' or 'ants plus brood'. Genera and species were identified when found, or collected for subsequent identification.

RESULTS

A total of 1 885 faecal subsamples has been analysed. The geographical distribution of sample collecting points is shown in Fig. 9. A list of genera and species of ants found in these samples is given in Table 4. The list, though reasonably comprehensive, is not finite because further sampling from a wider spread of localities within the woodpecker's range would certainly yield more species and possibly additional genera. The species list for the genus Camponotus is certainly incomplete. Camponotids are soft-bodied ants and very seldom survive passage through the woodpecker's digestive system without extensive dismemberment.

Fifty or more diet samples from any one site have yielded 9 - 17 genera and 12 - 30 species of ants. Collection of ants from study areas has shown that Ground Woodpeckers eat very nearly all the species of ants found to be present and usually also species that the various sampling techniques have failed to detect. These woodpeckers are without doubt very efficient samplers of ant fauna.

Table 5A gives the percentage frequency of occurrence of ant genera in all subsamples analysed. On average, 95% of the diet of the Ground Woodpeckers studied was derived from the genera Camponotus, Anoplolepis, Acantholepis, Crematogaster, Tetramorium, Pheidole, Meranoplus and Solenopsis. Representation of the different ant genera in the

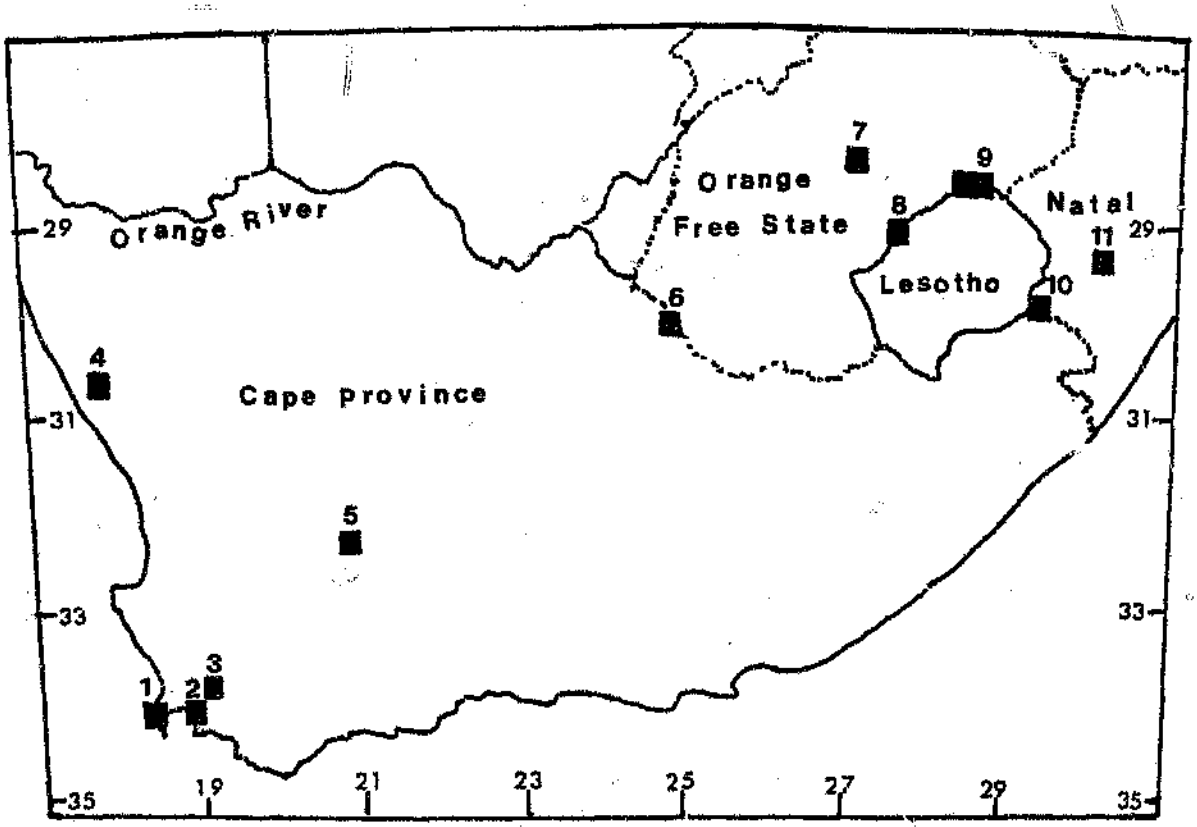

Figure 9. Quarter-degree squares in which Ground Woodpecker faecal samples were collected: 1. Elsies Peak; Slangkop; Cape of Good Hope Nature Reserve (various localities). 2. Helderberg Nature Resrve; Sir Lowry's Pass. 3. Du Toit's Kloof. 4. 15 km north of Garies, Namaqualand. 5. Sutherland, Karoo. 6. Van der Kloof Dam. 7. Koranna-berg. 8. Wonderkop. 9. Golden Gate Highlands National Park (various localities). 10 Castledene. 11. Carlisle, Dargle; Wellington Farm.

TABLE 4. List of genera and species of ants found in faeces of Ground Woodpeckers

DORYLINAE		Tetramorium	akermani
Dorylus	helvolus		bothae
Aenictus	sp.		capense
PONERINAE			erectum
Hagensia	sp.		frigidum
Bothroponera	sp.		muralti
Mesoponera	sp.		quadrispinosum
Leptogenys	nitida		sericeiventre
	peringueyi		setigerum
Trachymesopus	wroughtoni		setuliferum
CERAPACHYNAE			solidum group
Cerapachys	afer		sp. novum
	peringuey	Solenopsis	punctaticeps
	wroughtoni	Meronoplus	peringueyi
MYRMICINAE			
Myrmicaria	nigra		
Messor	capensis	DOLICHODERINAE	
Pheidole	capensis	Technomyrmex	albipes
	foreli	Iridomyrmex	humilis
	tenuinodis		
Rhoptromyrmex	globulinodis	FORMICINAE	
	transversinodis	Anoplolepis	custodiens
Crematogaster	arborea		steingroeveri
	kneri group	Plagiolepis	sp.
	liengmei	Acantholepis	capensis
	melanogaster	Camponotus	dicksoni
	natalensis		eugeniae
	peringueyi		maculatus
	rectinota		nasutus group
	transvaalensis		niveosetosus
Monomorium	albopilosum		rufoglaucus
	delagoensis		scaleris
Ocymyrmex	barbiger		thales
	weitzeckeri		sp. novum

Table 5A. Percentage frequency of occurrence of ant genera and other insecta in Ground Woodpecker's faeces from different localities. WLTN = Wellington; CSDN = Castledene; GCNP = Golden Gate Nat. Park; DMBL = Dumblane; WNKP = Wonderkop; VDKD = Vanderkloof Dam; ELKP = Elsies Peak; SUND = combined samples from sundry localities individually represented by less than 50 samples.

SITE	WLTN	CSDN	GCNP	DMBL	WNKP	VDKD	ELPK	SUND	TOTAL	Over. %
No. of samples	76	55	635	76	80	152	667	144	1885	
CAMPONOTUS	98.7	90,9	74,6	94,7	96,3	19,1	72,4	81,3	1377	73,1
ANOPLOLEPIS	80,3	-	47,9	52,6	97,5	80,9	88,9	63,9	1291	68,5
ACANTHOLEPIS	56,6	34,5	81,4	96,1	96,3	13,8	45,9	45,8	1122	59,5
TETRAMORIUM	64,5	49,1	67,6	86,8	42,5	9,2	38,5	31,9	922	48,9
CREMATOGASTER	93,4	100,0	26,0	-	62,5	82,2	54,9	33,3	880	46,7
PHEIDOLE	10.5	30,9	68,3	97,4	86,3	11,8	25,9	40,3	851	45,2
SOLENOPSIS	11,8	54,5	51,3	94,7	18,8	4,6	21,2	4,9	612	32,5
MERANOPLUS	69,7	25,5	39,8	-	81,3	-	17,2	19,4	594	31,5
MONOMORIUM	2,6	25,5	0,2	-	2,5	48,7	2,1	10,4	122	6,5
DORYLUS	11,8	3,6	6,3	-	38,8	-	1,9	5,6	103	5,5
OCYMYRMEX	-	-	11,0	-	-	-	-	0,7	71	3,8
MESSOR	-	-	3,1	-	-	3,9	-	6,3	35	1,9
CERAPACHYS	-	-	0,5	-	-	-	2,5	7,6	31	1,6
BOTHROPONERA	9,2	-	-	-	-	-	-	2,1	10	0,5
LEPTOGENYS	-	-	0,9	-	-	-	0,4	-	9	0,5
RHOPTROMYRMEX	-	-	-	-	2,5	-	0,7	0,7	8	0,4
MYRMICARIA	-	-	-	-	-	-	0,1	3,5	6	0,3
PLAGIOLEPIS	-	-	-	-	-	-	0,3	0,7	3	0,2
AENICTUS	-	-	-	-	-	0,7	-	1,4	3	0,2
TRACHYMESOPUS	-	-	0,2	-	-	-	-	-	1	0,1
TECHNOMYRMEX	-	-	-	-	-	-	0,1	-	1	0,1
IRIDOMYRMEX	-	-	-	-	-	-	0,1	-	1	0,1
BROOD	1,3	-	19,8	77,6	5,0	5,3	54,4	18,1	587	31,1
ALATES	19,7	3.6	29,6	73,7	3,8	2,0	23,2	28,5	463	24,6
TERMITES	17,1	12,7	8,0	-	7,5	16,4	1,9	4,9	116	6,2
BEETLES	-	3,6	1,4	-	6,3	-	2,1	4,2	36	1,9

birds' diets varies markedly even between neighbouring groups of Ground Woodpeckers, as for example between the Brandwag and Holkrans groups in the Golden Gate study area (Table 5B).

TABLE 5B. Diets of neighbouring Ground Woodpecker groups

GENUS	Brandwag N = 375	Holkrans N = 127
Acantholepis	80.5	69.3
Camponotus	71.2	91.3
Pheidole	78.9	37.0
Tetramorium	70.1	53.5
Solenopsis	54.7	31.5
Anoplolepis	43.5	52.8
Meranoplus	37.6	64.6
Crematogaster	18.9	39.4
Ocymyrmex	4.0	28.3
Dorylus	5.3	5.5
Messor	3.2	0.8
Leptogenys	1.3	0.8
Monomorium	-	0.8
Cerapachys	0.3	-
Trachymesopus	0.3	-

Such differences may reflect the relative abundance of the different ants in the woodpeckers' territories or home ranges, and insofar as the aforementioned eight genera are concerned this is probably a valid assumption. But apparent exceptions do occur. Table 6 shows the results of surface sampling on Elsies Peak where Myrmicaria nigra was consistently the third most commonly encountered ant. Yet it was found present in only one of the 667 faecal samples (0.15%) from this area.

These results are explicable when the nesting habits of Myrmicaria and the feeding method of Ground Woodpeckers

are taken into account. I have never seen these woodpeckers gleaning ants from the surface of the substrate, be it ground, rock or tree. Their feeding activities are concentrated on locating subsurface ant nests which they can reach with their extensible, sticky tongues. The prime rewards of such specialization are the nutritious eggs, pupae and developing alates. These are often placed close to the surface under sun-warmed stones, rock or wood. However, Myrmicaria nigra usually places its nest under a bush and about 30 - 60 cm below ground level (A.J. Prins, pers.comm.); in such a situation it is entirely inaccessible to Ground Woodpeckers. I have only once found an inhabited gallery of a Myrmicaria colony beneath a stone. This ant is commonly to be found foraging on the surface of the ground throughout the daylight hours and is comparatively slow-moving; its very low representation in woodpecker faecal samples supports the evidence gained from field observations of feeding birds that Ground Woodpeckers are not surface gleaners.

TABLE 6. Results of surface sampling of ant genera at Elsies Peak

GENUS	Number collected (N = 605)	Percentage of total	No. samples in which present (N = 14)	Percentage occurrence in samples
Anoplolepis	211	34.9	13	92.9
Camponotus	109	18.0	14	100.0
Myrmicaria	80	13.2	13	92.9
Pheidole	63	10.4	10	71.4
Acantholepis	52	8.6	12	85.7
Crematogaster	30	5.0	11	78.6
Tetramorium	27	4.5	10	71.4
Ocymyrmex	21	3.5	5	35.7
Iridomyrmex	10	1.7	7	50.0
Tetraponera	2	0.3	2	14.3

Further evidence that Ground Woodpeckers feed directly from ants' nests was provided by very small mites of the genera Oplitis and Leonardiella found in 17% of the faecal samples. These belong the Trachyuropodidae, a family known to associate with ants, residing in their nests and feeding on the detritus of the ants' food.

Table 6 includes one genus, Tetraponera, which has not yet been found in the Ground Woodpecker's diet. The species collected on Elsies Peak, Tetraponera clypeata, is a very slender ant; according to Skaife (1961):

"It makes its nests in dry stems with pithy centres, such as the flower-stalks of watsonias and aristea, hollowing out a long, narrow tunnel down the middle of the pith that is only just about wide enough to allow two of these slender-bodied insects to pass each other."

The pithy stalks of such annuals would probably not support the 125 g mass of the Ground Woodpecker and I have never seen them investigating such sites.

Table 7 gives the results of sampling under stones. In terms of genera found and their order of abundance, these results yield a better match with the woodpeckers' diet than do the results of surface sampling. Disparities are to be expected since the birds also probe crevices in rocks and trees and forage on the ground away from the immediate vicinity of rocks and stones.

Table 8 gives an indication of the seasonal distribution at Elsies Peak of ant brood and alates based on the results of surface sampling under stones and on the examination of Ground Woodpecker faeces. It is noteworthy that in the faecal samples the frequency of brood occurrence declines from January to July, whilst the incidence of alates shows an opposite trend. The presence of alates under stones was not scored separately from brood during sampling; often both occurred together.

A further indication of the Ground Woodpecker's propensity to find and eat ant brood and of the importance of such food was provided by the examination of the stomach contents of a bird killed in April 1984 in a collision with a motor vehicle in the Cape of Good Hope Nature

TABLE 7. Ant genera found under stones at Elsies Peak.

GENUS	Number collected (N = 260)	Percentage of total	No. samples in which present (N = 15)	Percentage occurrence in samples
Anoplolepis	96	36.9	14	93.3
Pheidole	42	16.1	11	73.3
Camponotus	33	12.7	14	93.3
Acantholepis	30	11.5	11	73.3
Tetramorium	28	10.8	11	73.3
Solenopsis	14	5.4	6	40.0
Technomyrmex	10	3.8	8	53.3
Cerapachys	2	0.8	2	14.3
Leptogenys	1	0.4	1	7.1
Myrmicaria	1	0.4	1	6.7
Iridomyrmex	1	0.4	1	6.7

TABLE 8. Seasonal availability of ant brood and alates at Elsies Peak as indicated by sampling under stones and from analyses of Ground Woodpecker faeces

MONTH	JAN	FEB	MAR	APR	MAY	JUN
UNDER STONES % ants with brood and/or alates	0.0	26.1	36.8	57.1	31.3	36.4
FAECAL ANALYSES						
No. of sabsamples	79	82	64	102	99	51
% containing brood	96.2	93.9	76.6	43.1	29.3	25.5
% contain. alates	8.9	14.6	12.5	24.5	30.3	29.4
MONTH	JUL	AUG	SEP	OCT	NOV	DEC
UNDER STONES % ants with brood and/o. alates	37.5	33.3	60.0	62.5	34.8	7.7
FAECAL ANALYSES						
No. of subsamples	26	38	15	8	19	24
% containing brood	3.8	0.0	0.0	12.5	31.6	50.0
% contain. alates	57.7	26.3	20.0	50.0	42.1	25.0

Reserve. In addition to worker ants of six different species, the stomach contained large numbers of alates and 1 420 eggs of Crematogaster peringueyi together with numerous pupae, nymphs and callows.

As one would expect, the Ground Woodpecker appears relatively tolerant of the attacks of the ants whose nests it is plundering. The bird mentioned above as a road casualty, had the head of a Crematogaster worker attached to one of its tail feathers, the jaws of the ant firmly locked around the shaft. Crematogaster ants (known in vernacular as 'cocktail ants' because of their habit of carrying the abdomen in a vertical position when excited) are aggressive in defence of their nest and, unless inhibited by low ambient temperature, swarm out over the surrounding area in a seething mass to bite any foreign object or body within reach. Pugnacious ants (Anoplolepis sp.) are well named and behave in similar fashion but move much faster and are bigger and better armed with sharper, more pointed mandibles, as befits their predatory behaviour. A probing woodpecker appears to be oblivious to the attacks of the defending ants, and remains motionless with beak tip buried in the access point whilst busily tongueing the nest inmates and brood into its mouth. When it has finished feeding, it will fly to a perch and there start to pick off ants fastened to its feet, legs or feathers.

P.A. Clancey has commented (in litt.) that Ground Woodpeckers have, in comparison with other southern African woodpeckers, "very long tongues and extremely viscous saliva." Both of these features are obviously functional attributes for their method of feeding. The viscous secretion of the salivary glands not only serves to turn the tongue into an effective sticky trap, but also incapacitates ants by gumming up their antennae. This probably applies particularly to the largest workers and soldiers which may attack the invading tongue. If one exposes the galleries of a large ant species such as, say, Camponotus maculatus, numbers of large workers and soldiers exceeding 12 mm in length are usually present. Remains of ants of

this size or larger have not been found in Ground Woodpecker faeces. It is possible that these large castes have the strength to match or exceed the adhesive tension of the saliva coating the woodpecker's tongue. More probably, however, they are excluded from the diet by a simple, physical constraint; if the width of the ant's head capsule is greater than the diameter of the muscular portion of the woodpecker's tongue it will be impossible to withdraw the ant through any passage forced by the tongue into the ant's nest.

Inspection of a Ground Woodpecker's feeding site immediately after the bird's departure from it will often reveal struggling ants attempting to free themselves of sticky adhering secretions and, sometimes, small worker ants rushing about in a disoriented fashion, carrying eggs or pupae. It is apparent that the ants have no effective defence against predation by these birds. At the same time it is evident that any one ant colony can withstand only so much plundering of its brood and work force. Colonies of Acantholepis capensis, for example, usually number only two or three hundred individuals (Skaife 1961). An average-sized faecal pellet of a Ground Woodpecker usually contains the remains of at least this many ants.

Field observations indicated that Ground Woodpeckers knew the precise locations of at least some ant nests in their home range. For example, one of a group of resting woodpeckers in the Injasuti area of the Natal Drakensberg suddenly took wing and flew some 200 m direct to a small outcropping rock in a footpath where it alighted and, after a few pecks, started to feed. Examination of the rock after the woodpecker had left it showed it to be covered with nighly agitated cocktail ants (Crematogaster sp.), all issuing from a crevice the woodpecker had probed. It was not possible for the woodpecker to see the rock from its original perch so it must have known of its locality and the fact that it was the site of an ant colony. A similar instance involved a one-metre-high limb of a Protea roupelliae tree to which one of a party of three woodpeckers made a direct flight and immediately

started to peck at and then to feed. Subsequent examination revealed Crematogaster ants swarming from a rothole in the limb. There were many Protea trees in the area and once again one got the impression that the bird flew directly from its rock to the one site which it knew contained food.

Such sites could not maintain their yield of food if they were exploited too regularly; it seemed likely that the woodpeckers probably 'did the rounds' within their home range, not staying in any one area for too long. Because of their habit of repairing to favoured rocks for resting periods, it was a relatively simple matter to check such rocks on a daily basis for faeces and thus to determine if the woodpeckers have been frequenting the area. This was done on Elsies Peak from April to mid-June in 1985. The results are summarised in Table 9 and show that the group (which numbered six at that time) did not frequent the monitored area for more than three consecutive days at a time. The periodicity observed was probably related to the size of the group; smaller groups might be expected to spend longer periods in favoured feeding areas. This was observed at Wellington where the two birds fed daily on a favoured section of a newly-burnt firebreak for many weeks.

TABLE 9. Frequency of area utilization by Ground Woodpecker group at Elsies Peak

	NUMBER OF CONSECUTIVE DAYS					
DAYS	1	2	3	4	5	>5
PRESENT	5	3	3	-	-	-
ABSENT	2	1	2	3	1	2

TABLE 10. Results of ant sampling transects within and outside of areas frequented by Ground Woodpecker groups

LOCALITY	Percentage of ant-positive strikes		
	Intensively utilized	Within home range of group	No Ground Woodpeckers
Wellington	11, 15	20	—
Castledene	—	23	—
Slangkop	—	22	—
Elsies Peak	12	—	—
Vergelegen - Natal	—	—	38
Blackhill, near E. Peak	—	—	38

Results of ant-sampling transects in Table 10 suggest that Ground Woodpeckers probably deplete ant populations in their territories. The Wellington firebreak yielded only 11% and 15% positive strikes in two transects after two months of daily feeding activity by two woodpeckers. The Elsies Peak footpath, intensively utilized by the local woodpecker group, yielded only 12% positive strikes whereas the Blackhill firebreak a few kilometres away, in an area not frequented by Ground Woodpeckers, gave more than three times the yield, as did an unburnt area in the Vergelegen Nature Reserve in Natal. Transects on areas within home ranges of Ground Woodpecker groups but not used intensively by them, gave intermediate figures. Although some other birds that share the woodpecker's habitat, notably chats and rock thrushes, also eat ants, such birds only take prey on the surface of the ground and do not feed exclusively on ants. The Ground Woodpeckers therefore experience no significant competition for their food resources from other birds and the apparent lowering of ant biomass within their territories must be due to their own exploitation.

The feeding posture of a Ground Woodpecker is distinctive and characterised by a stationary stance with the head down and the beak tip inserted into the substrate. Convulsive jerks of the tail such as given by some songbirds

when singing their loudest phrases provide the only indication of work being done by the woodpecker's tongue. The pecking which usually precedes insertion of the tongue into the hole or crevice may be to open or expose an ant nest access tunnel.

Ground Woodpeckers instinctively investigate any flaw, crack or hole in the substrate; this behaviour has been observed many times in the field and is a characteristic exploratory behaviour pattern in the young birds. A hand-reared juvenile concentrated its investigations on the interfaces between stones and the substrate in which they were embedded. Such interface areas are the usual sites of ant nest tunnels.

In the Ground Woodpecker the exploratory tapping is employed in the investigation of visually detected promising sites whereas in many arboreal woodpeckers tapping enables the bird to use the substrate as a sounding board to detect subsurface cavities that might contain food. When such cavities are detected the tapping changes to heavier blows as the bird chisels through the outer wood to expose the gallery. The Ground Woodpecker similarly employs heavy blows of the beak to dig into soil and thus obtain deeper penetration with its tongue when it finds a subterranean ant colony at the limits of its reach, but does not attempt such excavation into wood, as its beak lacks the chisel-tip characteristic of most arboreal woodpeckers. Ground Woodpeckers frequently forage in dead trees or on dead limbs of living trees which may provide nest sites for cocktail or other tree-dwelling ants. They are not as acrobatic as arboreal woodpeckers however, and I have never seen them hanging on the underside of horizontal limbs or branches, though they will sometimes cling to the sides of vertical trunks or limbs, using their stiffened central tail-feathers as props in true woodpecker fashion.

A sticky tongue is not a very discriminating device and although presumably armed with tastebuds there is probably not much the woodpecker can do to prevent ant nest detritus or small arthropods other than ants from

adhering to the exploring tongue. The majority of faeces examined contained only the remains of ants but fragments of other insects were found in some subsamples. These were either termites or beetles; their respective frequency of occurrence in subsamples is given in the last two rows of Table 5A.

Some beetles are obligate commensals of ant nests, such as Genuchus hottentotus, which is found in Crematogaster nests and Cossyphodes bewicki which is a guest of the pugnacious ant (Skaife 1961). Neither of these beetles has been identified in Ground Woodpecker faeces, but, as with ant remains, the coleopterans tend to be very fragmented. Most fragments found were derived from small to very small beetles; obviously the size of these insects cannot exceed the dimensions of the ant galleries and the same physical constraints of extraction from the access tunnel must apply. Semi-intact remains have permitted the identification of two families: two Pselaphidae from Holkrans and two larval Scarabaeids were found in an Elsies Peak sample. The amount of beetle material in relation to the amount of ant material found in the 36 subsamples was conservatively of the ratio 1:300; expressed as a percentage of the 1885 subsamples examined, Coleoptera make up only about 0.006% of the Ground Woodpecker's diet.

On the basis of these analyses it can be assumed that beetles are not significant in the diet and it is possible that they are accidentally ingested. This could happen if the beetles were inside the ants' nests, either as guests or as prey (whole or detrital) of predatory ant species. A third possibility is that in its search for ants a woodpecker may probe the larval chamber of a ground dwelling beetle and unavoidably 'capture' some of the inmates. The two scarab larvae from Elsies Peak suggest such a circumstance. Presumably the taste of inappropriate prey is wrong and the bird does not persist in probing the same hole.

Termites also are possibly ingested accidentally. When found in samples they usually occur in larger numbers than beetles so the ratio of termites to ants is higher, about

1:50 on average. In three subsamples (two from Natal and one from the Orange Free State) termites made up about one third of the identifiable material, the balance being of ants. Even in these cases however, the total number of termites present could have been captured with a single probe of the woodpecker's tongue into a well-populated termite gallery. All termite remains have been of workers and soldiers of two genera, Trinervitermes and Odontotermes. Mounds of the former genus are abundant features of some grassland areas within the range of the Ground Woodpecker in Natal and the Orange Free State. The woodpeckers often perch on the mounds at Wonderkop and in the Golden Gate National Park. Young, inexperienced Ground Woodpeckers could conceivably probe small vent holes in such mounds as they do any hole or crevice which they come across. Many species of ants actually make their nests in inhabited termitaria; Prins (1963) for example, records the ant genera Crematogaster, Pheidole, Ocymyrmex, Camponotus and Monomorium associating with termites in the Kruger National Park, the last mentioned genus with Trinervitermes. Sampling for ant nests under stones has sometimes revealed clusters of termite workers. Such encounters were low at Elsies Peak, occurring in four out of fourteen samples and being found under only one to three percent of the stones examined. In a single sample at Wellington however, termites were found under sixteen of the 100 stones checked, sometimes under the same stones as a small ant colony, though separated from it.

In the Golden Gate Park, R. Earlé (pers. comm.) watched a spectacular emergence of Trinervitermes alates after heavy rains in October 1985. Various species of birds converged on one mound to take the alates as they emerged from it. A group of three young Ground Woodpeckers (known to be sibs of the previous year and therefore approximately 12 months old) were attracted by the activity and also flew to the mound. It would have been easy for them to gorge themselves on termites and alates, but after a few desultory pecks they evidently lost interest and flew away again.

In the southwestern Cape the Black Mound Termite Amitermes sp. is the only Isopteran found in the Ground Woodpecker's habitat and its mounds are neither as prominent nor as abundant as the mounds of Trinervitermes in the summer rainfall area. Table 5A shows that the Elsies Peak faecal samples have the lowest incidence of termite remains of all sampling areas except Dumblane (from which only one sample batch was collected). R. Schmidt has reported (pers. comm.) seeing a Ground Woodpecker pecking away at a termite mound on Lions Head at Cape Town. Such activity could easily be taken to mean that the bird was hunting termites, but, as indicated above, it could have found ants, or it might have been investigating the mound as a potential nest site.

Many African insectivorous birds consume termite workers and alates avidly, and the alates are eaten by many additional species that are not typically insectivorous (as well as by many mammals, including man). It is, therefore, remarkable that Ground Woodpeckers, which are better equipped than most birds to exploit this food resource, evidently seldom, if ever, feed on termites by choice, and show little interest in emerging alates.

Termite-eating seems rare in picids, however. Short (1982) lists isopterans in the diet of only 7% of woodpecker species worldwide, and although this percentage might be higher if the diets of tropical species were better known, it is likely to remain insignificant next to the level of 60% of woodpecker species known to eat ants (Short 1982).

SUMMARY

The Ground Woodpecker is highly specialized in its diet and feeding habits. It feeds preferentially on ants and ant brood, and 53 species of 24 genera have been identified from the 1 885 faecal samples analysed. Eight ant genera contribute 95% of the food. Ants are not gleaned off the surface but are obtained by subsurface probing with the woodpecker's sticky tongue. This feeding technique places constraints on the kinds and size of the

ants eaten, but permits the woodpecker to feed on the smaller castes and nutritious brood of the majority of ant species occuring within its territory or home range. The woodpeckers learn the sites of ant colonies within their territories and there is some evidence to suggest that their depredations result in a lowering of ant biomass in intensively foraged areas. Because of its specialized feeding technique the Ground Woodpecker suffers no food resource competition from any other vertebrate species. In addition to ants, beetles and termites have also been found in the faecal samples analysed. Beetles occur in very small numbers and are probably accidentally ingested. Termites occur in larger numbers but still only constitute 0.12% of the identified material in samples. They are evidently not preferred food and are possibly also ingested by accident rather than with intent.

o o O o o

5. SIGNAL BEHAVIOUR

"This singular bird presents a remarkable instance of the adaptation of creatures to the localities wherein their lot is cast. ...They feed together and roost together in some deserted hole; and their loud, harsh cries, as they call to each other, may be heard to a considerable distance."

Edgar Leopold Layard (1867): The birds of South Africa.

INTRODUCTION

The ways in which animals signal their existence and intentions to others of their kind vary extensively with their form and life style. Birds perhaps exhibit the greatest variety of signal forms, employing visual and auditory displays in which colour, plumage patterns, posture, flight, vocalisation and mechanically produced sounds may be used singly or in combination.

Paterson (1985) has emphasised the fundamental importance of the train of co-adapted signals and responses by which potential mates of biparental eukaryotes recognise each other, and which he terms the Specific-Mate Recognition System (SMRS). The SMRS is not necessarily obvious to the human observer. Furthermore, it is by definition a species-wide trait, and because of coadaptation between the mating partners, the characters are stabilized (Paterson 1978; Henderson and Lambert 1982).

That is not to say that the SMRS cannot comprise, in part, an unvarying component of a display which does show local or regional variation. Most auditory displays serve dual or multiple functions; Emlen (1972) has commented that components of songs which involve i*ndividual* recognition (my emphasis) tend to be extreme*ly* variable. Hence a call which, in its basic form, serves as one of the series of co-ordinated signals of the SMRS, may feasibly

be embellished to serve the purpose of individual recognition without detriment to the functioning of the SMRS. This unvarying component will remain under strong stabilizing selection so long as the species remains within its normal habitat.

Signal behaviour will also evolve to fulfil functions such as communication between members of a pair or family group. In species which live in social groups and which therefore spend much time in close proximity to each other, signalling is often subtle. The Ground Woodpecker is not a truly sociable species, but family groups persist for some nine months.

This chapter sets out all the examples of signal behaviour that I have observed in the Ground Woodpecker. Obviously some of these incorporate components of the SMRS and inasmuch as any of these examples of behaviour differ from those patterns exhibited by other woodpeckers, they are likely to point to selection pressures operating at the time of speciation.

VOCALIZATIONS

The different calls of the Ground Woodpecker are listed here under transliterated labels rather than by function as some of them appear to serve more than one function. Sonogram facsimiles in Fig. 10 are from a composite tape compiled from various recordings by different people. Technical details of machines and microphones used are not known, and some spectrographic details may have been lost during copying.

The PEEURG call.

This vocalization (Fig. 10A) is commonly used as an alarm call. On such occasions there is sharp emphasis on the first part, the '<u>urg</u>' virtually suppressed, so that the call becomes a strident '<u>Peeerr</u>'. It is the characteristic challenge from a sentinel (see pp. 72-74) or from one of a resting group if an intruder of any kind enters the field of view. It is easy to confuse a distant (faint) rendition of this call with the '<u>Peeooo</u>' whistle of the

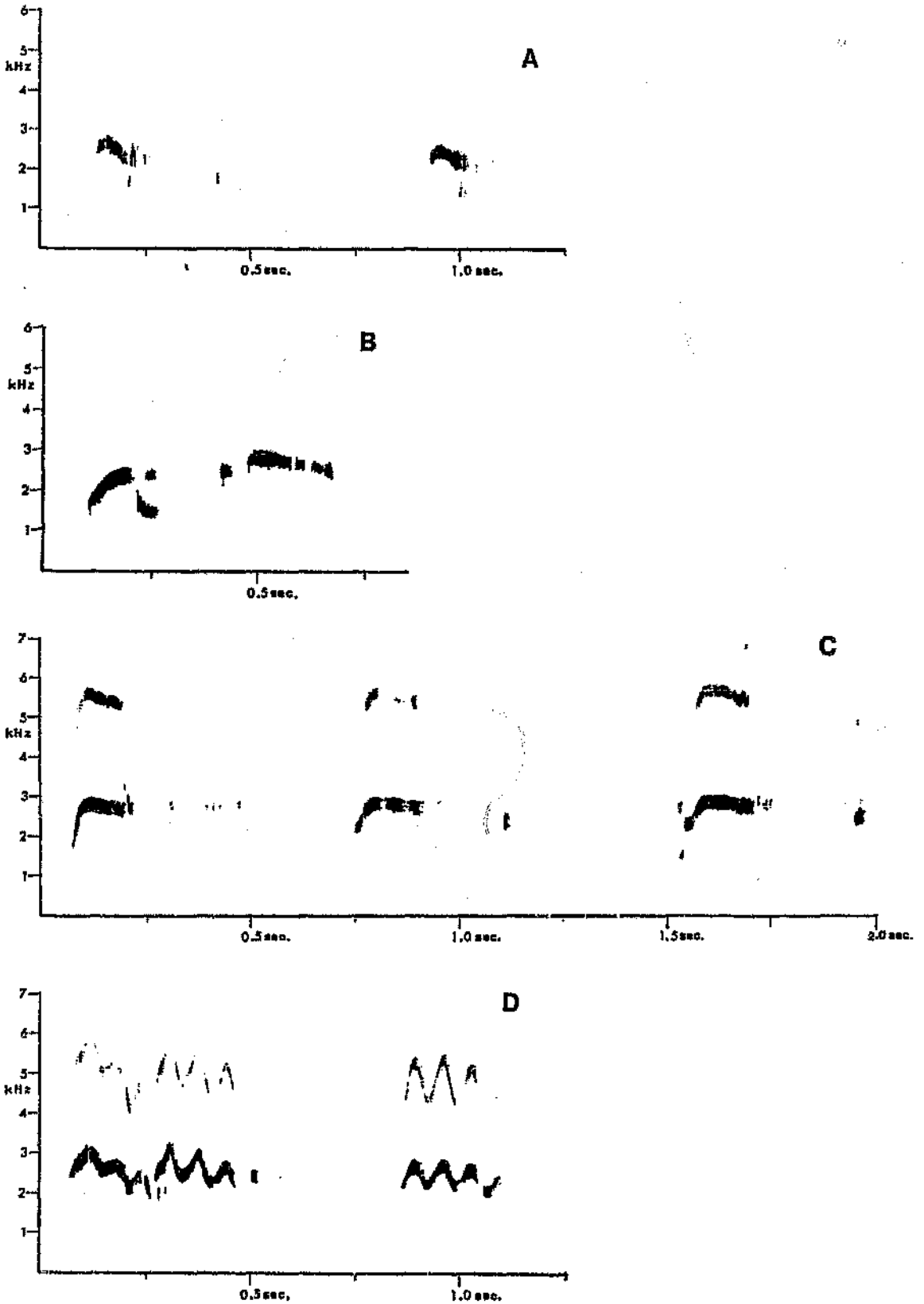

Figure 10. Sonograms of Ground Woodpecker calls: A, Peeurg alarm calls by adult; B, Redwinged Starling calls; C, Wee-chik call; D, 'Lanner' call.

Redwinged Starling Onychognathus morio (Fig. 10B), commonly sympatric with the Ground Woodpecker. The call is uttered very vociferously by all members of a group if a mammalian predator (such as a mongoose) is espied.

In lower intensity alarm, less emphasis is placed on the first part of the call and the second part becomes more audible. At this level the call is similar to the call of some seagulls (Larus spp.) and sufficiently like the alarm call of the Rock Hyrax Procavia capensis for an indistinctly-heard call of this mammal to be mistaken for that of the woodpecker.

In non-alarm situations the call is less strident and the 'urg' part is lengthened. Such a call may be uttered by a sentinel bird when other members of the group are foraging, or by a dependent juvenile in the close presence of a foraging parent. When the parent is foraging at a distance the peeurg call, uttered by the juvenile at frequent intervals (see Chapter 6), functions as a location call, enabling the adult to find the juvenile easily.

The 'urg' sound by itself is further employed in intergroup communication. For example, the Elsies Peak group of six birds watched resting on their favourite rock pile for some 70 minutes in the late afternoon on 20 January 1985 (pp. 3-4), eventually became restless and congregated on the topmost rock. At this stage there commenced a conversational growling amongst them - barely audible from my position 15 m distant. Each growl was in fact a quiet, gutteral 'burrgg' note, an obvious derivative of the peeurg call.

The WEE-CHIK call.

This double-syllabled call, usually repeated two or three times in any one sequence (Fig. 10C) appears to function primarily as a contact call. A bird which has flown by itself and settled at a point distant from its mate or other members of the group will usually call in this manner. A dependent juvenile will also intersperse its peeurg calls with an occasional wee-chik call. The call is far-carrying and unmistakable compared with dis-

tant peeurg calls which can be confused (by the human observer) with calls of other species. A foraging parent returning to a dependent fledgeling will also utter this call, with prompt vocal response from the juvenile.

The call may also be used in a territorial context to advertise presence because individual birds in resting groups will occasionally call in this manner.

The 'LANNER' call.

In my field notes I termed this the 'Lanner call' because of its resemblance to the kirr-eee call (Steyn 1982) of the Lanner Falcon Falco biarmicus. It is not an easy call to transcribe and may sound different to other observers. It is possibly the same vocalization as the tchew-kee call described by Short (1971d). A sonogram is provided in Fig. 10D.

It is used in a variety of situations and is most commonly uttered by a bird alighting after a flight of 50 m or more to a rock on which another member of the group is already perched, or by an alighting group to one another. It is also sometimes used in flight, but such occasions seem rare. It sounds like a high-intensity state vocalization and peeurg calls from an excited or agitated bird sometimes merge into 'Lanner' calls. A hand-reared juvenile only a few weeks old uttered these calls when being force-fed and the over-riding impression was that it was affronted at being handled and restrained; the call expressed annoyance and rebuke, but not panic.

DISPLAYS

Short (1971d), commenting on his relatively brief studies of southern African woodpeckers, stated that overt displays were rarely noted in Ground Woodpeckers and attributed this to the intimate association pertaining among individuals of a group.

Non-ritualized movements and displays observed in the course of this study will here be divided into two categories. In the first group are intention or anxiety movements which the bird uses in everyday situations. In the second

group are more ritualized movements and evident displays used in antagonistic encounters or mating ceremonies. In general, displays of the first group will be found to be widely shared at the sub-family level, whereas the mating ceremonies are likely to be unique, in at least some respects, to the species involved.

GROUP I.

Wing-flicking and head-dipping.

Wing-flicking involves a rapid (eye-blink speed) out-in movement of one or other wing and is employed in a variety of situations. In 37 recorded instances, 15 occurred prior to flight or movement on the rock after a period of inactivity and thus might be classified as flight intention movements. Conversely, eight observed instances occurred after flight, without the close presence of another bird, and in seven observed cases wings were flicked without prior or subsequent activity. One resting bird wing-flicked once prior to preening and another prior to scratching. Two cases were recorded in anxiety situations (though it was not determined what had alarmed the woodpecker) and in three cases predator abuse (mobbing behaviour) involved extensive wing-flicking.

The head-dipping or bowing movement is likewise used in anxiety situations and is sometimes employed in place of, as well as in addition to, wing-flicking. It was most commonly observed during mammalian predator mobbing episodes (eight records). The balance of records (of a total of 23) involve four cases prior to flight, one before and one after drinking and two cases after copulation. This movement may be derived from a pecking movement; it is perhaps significant that in one instance of high-intensity mobbing behaviour when a group of woodpeckers had detected the approach of an Egyptian Mongoose (page 70), redirected pecking of the substrate was observed. In such instances the woodpeckers are not overtly displaying to each other so much as engaging in group predator-mobbing behaviour.

GROUP II.

Antagonistic display.

I have only once observed a real dispute between Ground Woodpeckers and this occurred at Dargle in November 1979 when two foraging groups evidently encountered each other at the common boundary of their repective territories.

The one group was under observation on a rocky slope at 16h10. It comprised two adults and two juveniles which had fledged some eight weeks previously. Some of the birds were foraging. Quite suddenly chaos seemed to break out. There was chasing, accompanied by loud vocalizing, mainly Lanner calls. At one stage there were six birds in view simultaneously with others calling 'off stage'. One bird was frequently chasing and supplanting another; they went back and forth but the movements were so rapid, with frequent momentary disappearances behind boulders, that it was impossible to see whether pursuer and pursued swopped roles at any stage. There were two aerial flights with near grappling, both combatants flying up and pecking at one another, much in the manner of a bird fighting its reflection in a window. When perched, the typical posture was as sketched in Fig. 11a, the bird sleeked, neck outstretched and bowed concavely, tail slightly fanned, occassionally and very briefly cocked. The throat feathers were erected and looked dark by comparison with the chest and lower parts; in fact the whole head appeared dark and with a perpetually open beak (to display black gape perhaps or alternatively panting with exertion) the pale-coloured eye contrasted well.

I could discern no obvious display of the carmine-coloured plumage on belly or rump during these encounters, nor was it possible even to determine which sexes were involved. My attention was on the main combatants and the impression was that some of the other birds were merely perched and watching. There were two bouts of such behaviour, separated by a couple of minutes, before the groups parted permanently. It was not possible to determine how many woodpeckers were in the other group.

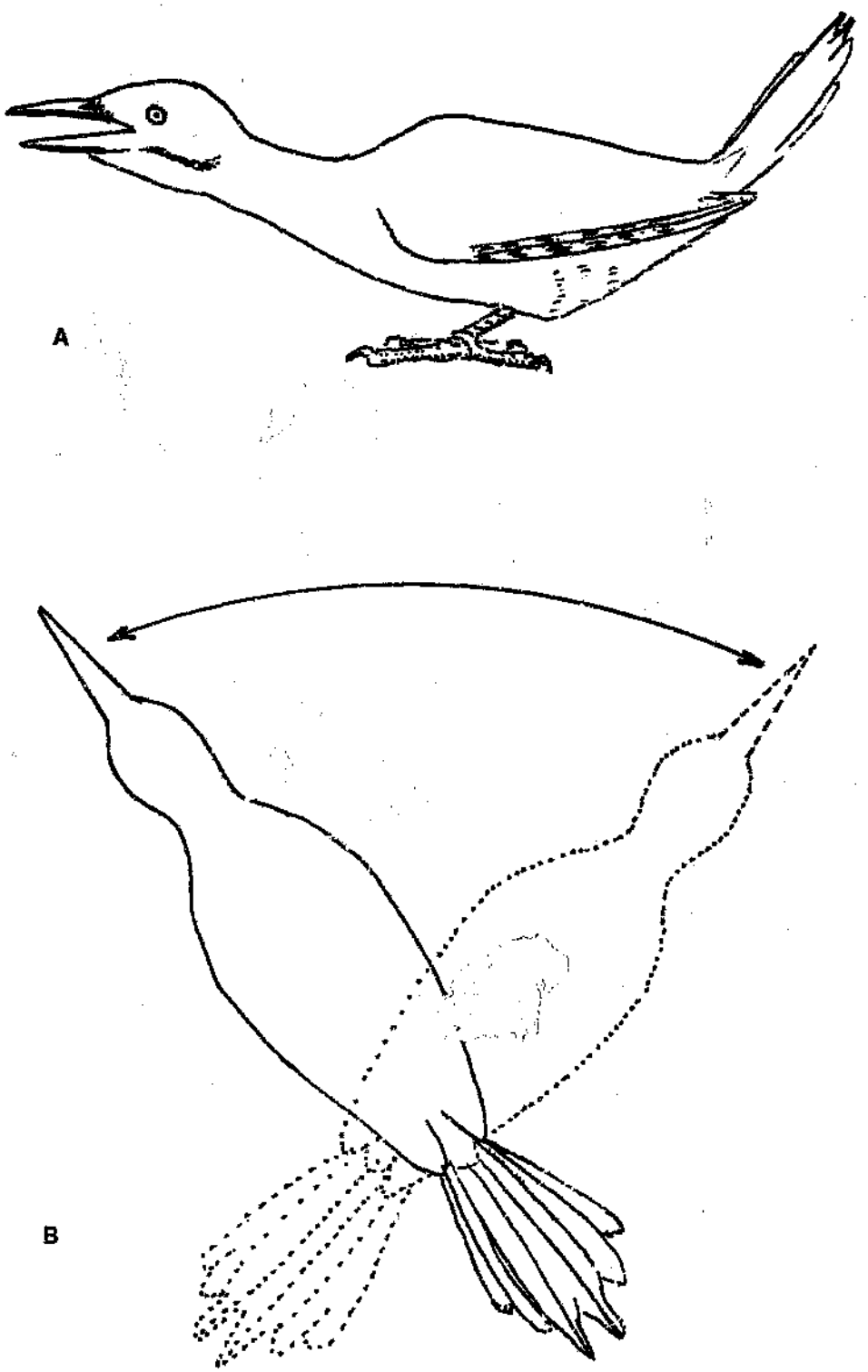

Figure 11. Postures used by Ground Woodpeckers in aggressive encounters; A, lateral view of threat display; B, dorsal view of 90° swinging display.

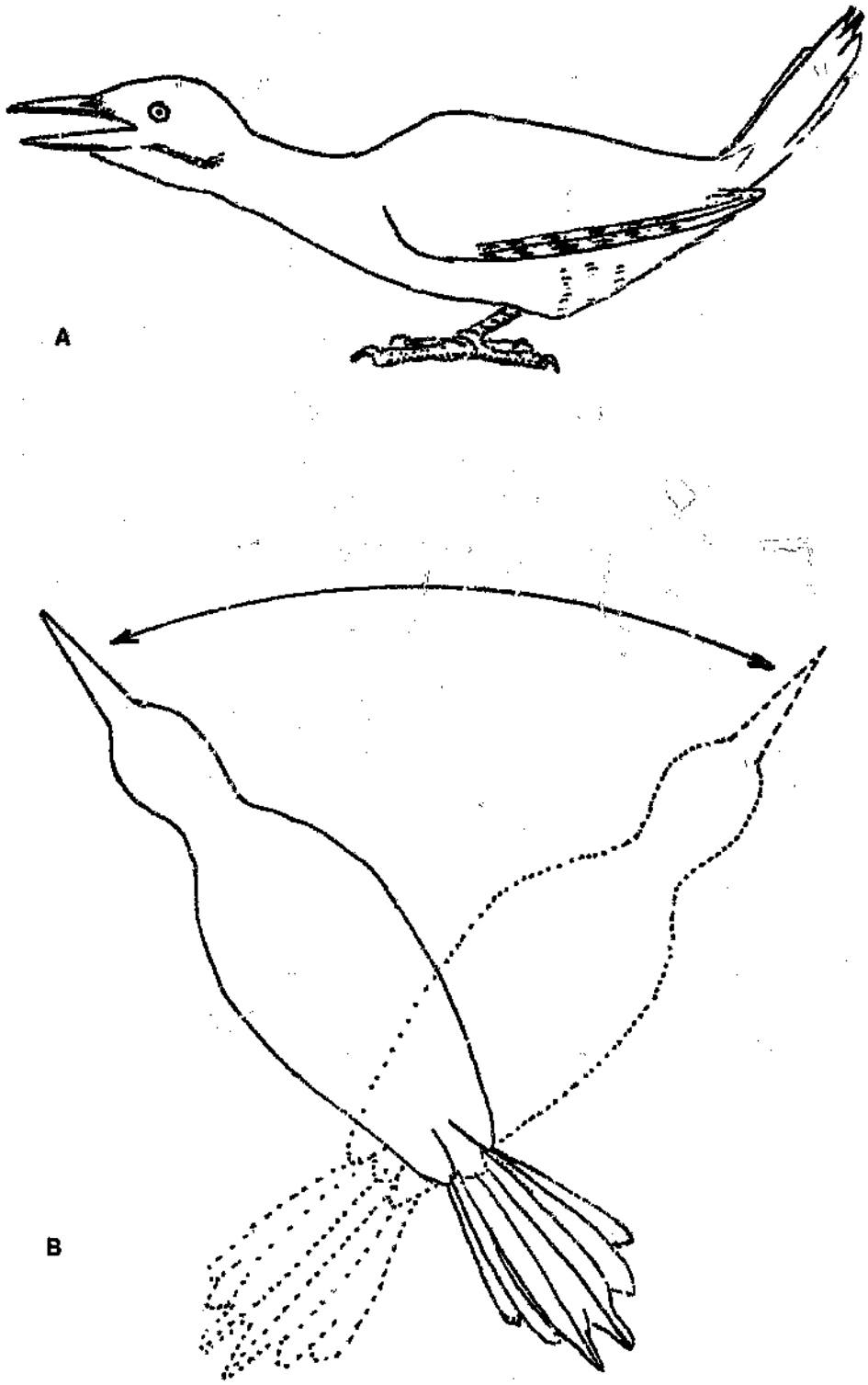

Figure 11. Postures used by Ground Woodpeckers in aggressive encounters; A, lateral view of threat display; B, dorsal view of 90° swinging display.

Because natural encounters of this type were so rarely observed, it was necessary to contrive a situation in which a wild Ground Woodpecker was confronted with a potential conspecific interloper. This was achieved at Elsies Peak by positioning a stuffed model on a favourite rock. After several unsuccessful attempts, a single bird (an adult female) was attracted by a tape-recording of the peeurg call. She landed on the slope of the rock below the model. Her plumage was sleeked, tail partially fanned and depressed to the rock, and the beak, head and body, viewed dorsally, were held in a straight line. She started head-dipping and wing-flicking and commenced 90° swinging moves. In these moves the bird stood at about 45° to the model, then pivoted through 90° to pose at 45° on the opposite quadrant (Fig. 11b). When posing at 45° the malar stripe is shown to advantage. There was no vocalizing and no beak opening or gaping. The beak and head were held elevated showing the pale whitish throat to advantage (Fig. 12a). After moving around the model, the woodpecker attacked it from the one side, pecking at the face (Fig. 12b). Then she leapt onto the back of the model and started raining blows on the skull (Fig. 12c). At this point I intervened, fearing that she would damage the model beyond repair.

Short (1971d) mentioned a head-swinging display. However, in the display described above the head is kept in a straight line with the back and tail and the whole body pivots. I have observed similar displays from resting Ground Woodpeckers in response to tape-recorded vocalizations. Without leaving its rock the responding bird has pivoted first one way and then the other, viewing the source of the sound alternatively from either eye.

Display flight.

The normal flight of the Ground Woodpecker is a dipping, seemingly 'heavy' flight with audible wingbeats, typical in fact of many woodpeckers. A characteristic of this species however, is a display flight which may serve to advertise territory but also often precedes copulation

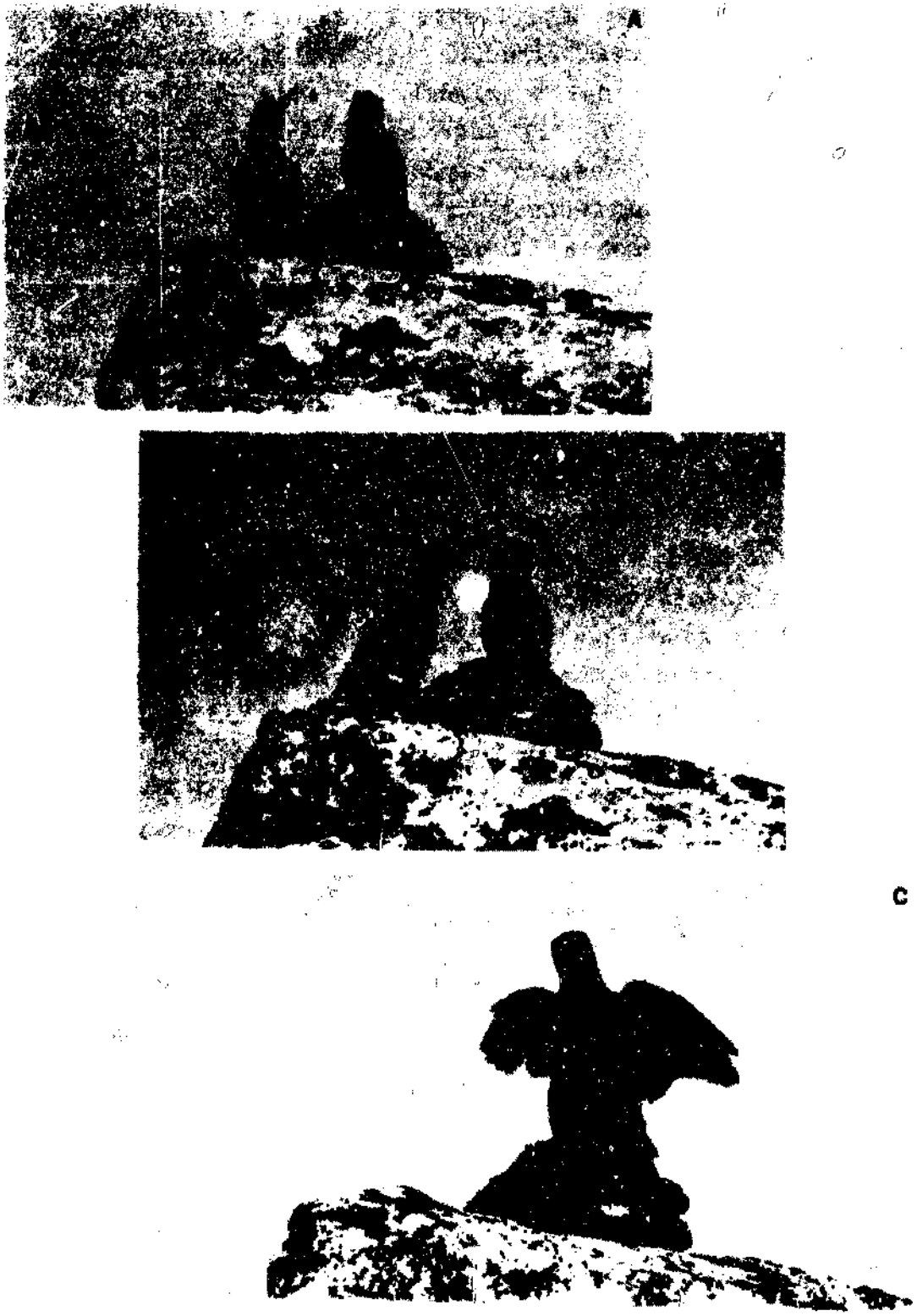

Figure 12. Adult female Ground Woodpecker approaching and attacking model; Elsies Peak.

or copulation attempts. Typically, a bird, presumably the male of a mated pair, will suddenly leave a resting group and commence an erratic, jinking flight to the accompaniment of loud peeurg calls. The flight may take the bird temporarily out of sight over ridges, or it may zigzag back and forth in front of the perched mate and group. The flight usually lasts less than 15 seconds and frequently culminates on landing with wee-chik or 'Lanner' calls, followed by the pre-copulatory display.

The 'Kingfisher' display and mating ceremony.

This display usually precedes successful copulation attempts, particularly after the erratic display flight described above. The displaying bird stands erect in front of the female and holds out both wings. I have termed this the Kingfisher display beacause it is reminescent of the open-wing display of some Halcyon kingfishers. The female, if receptive, turns away in a submissive posture with head held low and horizontally and with wings slightly drooped, thus exposing the carmine patch on the rump. The upright, spread-wing posture of the mal displays the carmine lower chest and belly plumage to advantage. The wings, though not strikingly patterned as in Halcyon Kingfishers, do have contrasting, bright yellow flight feather shafts on the underside as well as the upperside. This feature is not shared with other southern African woodpeckers, whose underwing feather shafts are dull and lacking in contrast.

In a successful copulation (observed ten times in this study) the male mounts the back of the female (who has submissively turned away from him as aforementioned) and gradually falls over to the left side where he lies momentarily with both wings spread; in this position the left wing is usually lying on the rock and the right one is extended upwards. Copulation attempts which do not end in this fashion are frequently followed by some sort of redirected activity (such as bill wiping) and are presumably unsuccessful. The copulation observed and described by Short (1971d) was probably an example of unsuccessful coition.

PREDATOR AVOIDANCE BEHAVIOUR

A striking aspect of Ground Woodpecker behaviour concerns overt and evident precautionary measures adopted to avoid predation. Potential predators can be divided into two classes, aerial and terrestrial, and reactions to encounters vary according to which is involved.

No instances of actual predation on Ground Woodpeckers have been observed, but the birds reactions to potential predators leaves little doubt that aerial predators, especially falcons, are the most feared. The passage of a Lanner Falcon as much as 500 m distant will cause woodpeckers squatting on a rock to sidle down its hidden face. A close pass by a falcon or indeed by any raptor will result in all of the group precipitately leaving their positions and scuttling under the rock; it is probably no coincidence that rocks favoured for resting usually have easily accessible hollows or crevices beneath them. The woodpeckers' behaviour in such instances is identical to that adopted by Rock Hyraxes Procavia capensis which sun themselves on exposed rocks but scuttle down into crannies amongst the piled boulders at the approach of danger. Ground Woodpeckers and hyraxes may occasionally be seen resting together on the same rock, though the woodpeckers will usually vacate the rock if a hyrax approaches too closely.

The act of taking cover is not normally accompanied by any vocalizations, perhaps because the birds could increase the danger by drawing attention to themselves; in any event the close proximity of members of the group ensures that precipitate movement by one bird alerts the others. An actual attack or near miss by a raptor evokes actual shrieks from the woodpeckers, a response very akin to human behaviour in similar situations. One such incident was witnessed on Elsies Peak in August 1984. A pair of woodpeckers were preening vigorously on a rock apex overhanging a cliff face at the end of a rock ridge. After some five minutes one woodpecker uttered a peeurg call and both birds dived off their perch and were lost to sight below the edge of the cliff. Seconds later a Redwinged Starling arrived and landed where the woodpeckers had been

perched, but it took flight again after some 20 seconds. One of the woodpeckers then re-appeared and perched on the exact spot vacated by the starling, looking in a south-westerly direction. It suddenly turned and flew down over the north-facing cliff edge and seconds later a Rock Kestrel Falco tinnunculus stooped past the pinnacle. This stoop was certainly at the woodpecker, though it may have been in play because the speed of the stoop was much faster than that of the controlled parachute-like drop (Steyn 1982) by which the Rock Kestrel normally takes prey. I could not even be sure that the woodpecker had seen the approaching Kestrel since at no time did it look up in the direction from which the hawk had stooped. After the Kestrel had flashed past there was a loud, shrieking peeurg followed instantly by a high-pitched, real shriek which led me to wonder whether one of the woodpeckers had been caught by the Kestrel on the cliff face. I made my way to the pinnacle and from that vantage point was able to see both woodpeckers sitting on a ledge of the cliff face showing no signs of alarm.

Any low-flying bird will alarm the woodpeckers if it comes upon them or over them suddenly. On Elsies Peak on a sunny June afternoon a group of three Ground Woodpeckers tumbled off their rocks and sought temporary cover in a crevice when a flying Rock Martin Hirundo fuligula came around a boulder very low down and straight at them. This bird had been foraging in the vicinity for some time and the woodpeckers were quite unperturbed by it, but its sudden close appearance and low-level, fast, approach triggered predator avoidance tactics.

The slow approach of non-raptorial birds does not usually result in predator-avoidance behaviour, but one incident was observed in Glencairn in which all the norms of Ground Woodpecker behaviour appeared to be violated. Early one morning in January 1985, some shrieky 'peeurg' calls were heard from the marsh when a Hamerkop Stork Scopus umbretta flew low over the reeds towards the sea, labouring into the teeth of a strong southeasterly wind.

While the Hamerkop was still about fifty metres distant from them, a group of four Ground Woodpeckers, two adults and two young, flew up from the reedbeds with a wild chorus of peeurg notes and perched briefly on the roof of a house before flying on up to the rock-strewn firebreak on the hillside, where they stopped calling and were quickly lost to sight.

This incident provides a genuine example of the exception that proves the rule. It might reasonably be presumed that the woodpeckers mistook the low-flying stork for a Steppe Buzzard Buteo buteo, since the two species are of similar size and colouration and there is a visiting Buzzard which frequents the Glencairn valley and slopes of Elsies Peak in the summer months. Whatever the case, the woodpeckers' behaviour was uncharacteristic in that they initially drew attention to themselves by loud vocalisations and by flight movement. However, reedbeds are atypical habitat for the species and the Glencairn marsh contains no rocks which the woodpeckers could have hidden behind or beneath. The loud calls probably served to alert the young birds to the approach of danger and the two-stage flight took the group directly to the nearest rocky area. Had the approaching bird been a falcon or goshawk, the woodpeckers' response would have been inappropriate and possibly fatal for one of their group.

Responses to terrestrial predators are rather different and the term "predator abuse" is more descriptive than "predator avoidance". Two instances have been observed, both involving mongooses.

The first was at Coleford in June 1980. I was watching one woodpecker perched on a rock above a waterfall when my attention was drawn to a commotion further up the slope. The other five woodpeckers in the group were uttering strident peeurg calls as an Egyptian Mongoose Herpestes ichneumon came slinking down through the short grass. It skirted the waterfall, keeping to the steep grassy slope at one side. All six of the woodpeckers followed its progress, eventually perching on the basalt slabs flanking the waterfall, looking down on the mongoose and giving

loud peeurg calls to the accompaniment of much head-dipping. They only quietened when the mongoose had disappeared from view further down the slope and they made no attempt to follow it.

The second incident was seen at Wellington, during the same month. At 15h30 the two woodpeckers, which had initially been resting, flew from their rock and crossed the firebreak to land on another group of rocks which were also a favoured resting place. No sooner had they arrived however, than they broke out into a clamour of peeurg and 'Lanner' calls. The cause of the excitement was a large Slender Mongoose Herpestes sanguinus which I glimpsed briefly amongst the rocks. The woodpeckers went on abusing it for seven minutes and such was their outcry that birds of several other species - longclaws, cisticolas, widowbirds and a Fiscal Shrike Lanius collaris all converged on the spot. They did not take part in any mobbing however, perhaps because they did not see the mongoose which had either holed up under the rocks or slipped away under cover of the surrounding rank vegetation.

Because these woodpeckers spend a lot of time on the ground when feeding, and grass and other vegetation limits their field of view, diurnal mongoose species, opportunistic predators at all times, are probably the most dangerous terrestrial enemies.

Snakes must also constitute a risk and although there are relatively few preferentially bird-eating species within the woodpecker's geographical range, the Spitting Cobra or Ringhals Hemachatus haemachatus and the Cape Cobra Naja nivea are both potential predators. The Cape Cobra, although only found in the western half of the Ground Woodpeckers' range (it is not known to occur much east of 28°E) may even be a significant predator because of its partiality for dry gullies and its propensity to investigate and live in rodent and other animal holes (Fitzsimons 1962). The Puffadder Bitis arietans, although primarily a rodent-eater, is also an opportunist predator of birds (Rasa 1985) and is a common reptile in the Ground

Woodpecker's habitat throughout southern Africa.

Although a natural encounter between a Ground Woodpecker and a snake has not been observed, resting woodpeckers startle easily if a Cordylus lizard climbs up over the edge of their rock to sunbathe. More significant perhaps is their behaviour when going to roost. The first bird to fly to the roosting tunnel may sit hunched at the entrance for as long as five minutes before entering. Once inside, remaining members of a group tend to pause at the entrance for only short periods or not at all. Such behaviour is most simply explained as a means of checking (by listening?) that the roosting burrow has not been occupied during the birds' absence by some other animal, be it bird, mammal or reptile. Similar caution is displayed by the Great Spotted Woodpecker Dendrocopus major which will avoid a roost hole if it hears the grumbling of an Edible Dormouse Glis glis within (Cramp 1985).

Avoidance of perceived potential predators is a normal behaviour pattern documented for a wide range of prey animals and is not particularly remarkable. However, posting lookouts to give early warning of the approach of danger is a strategy seldom encountered, and is rarer in birds than it is in mammals. Sentinel behaviour is, however, well developed in the Ground Woodpecker and is invariably manifested by a solitary bird occupying an elevated perch in the immediate vicinity of a foraging mate or group.

When only two birds compose a group, early morning and late afternoon feeding may be pursued without either bird acting as a look-out, presumably because the need to feed adequately at such times outweighs the risk of foraging without sentinels. But between these two periods, alternate foraging and sentinel behaviour seems compulsive and extensive observational data demonstrates regular exchanging of roles between the two birds (Fig. 12D). The foraging bird flies up from the ground to join its mate and often beak-wipes vigorously. The mate then descends to the ground to forage. After several minutes the process is repeated, and the exchange of roles continues until both

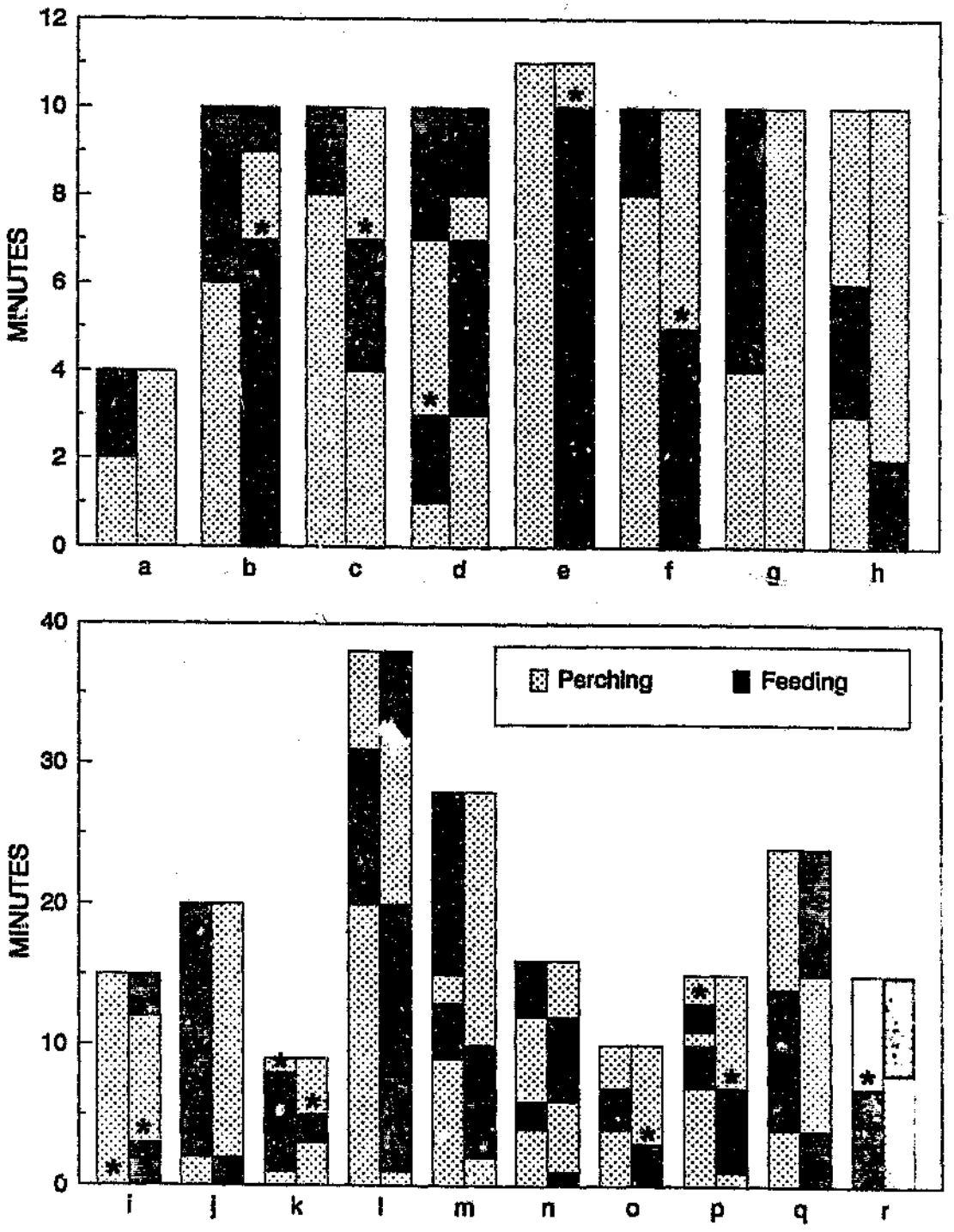

Figure 12D. Alternate foraging behaviour by two Ground Woodpeckers, March–July 1980. The perched bird acts as the sentinel. Asterisk = beak wiping. Periods b and d commenced at 16h58 and 17h31 respectively (near sunset); other periods started between 08h29 and 16h00.

birds have foraged sufficiently, after which they may rest together on a rock for an extended period. When the groups are larger, sentinels can be seen even during peak feeding periods in the late afternoon, though at such times change-overs tend to be more frequent. It is difficult to collect quantitative data in groups of more than two birds. Change-overs are easily observed but inability to identify individual group members prohibits determination of whether all or only some group members are on the sentinel roster.

The evidence for sentinel behaviour set out in Fig. 12D represents 18 observation periods totalling 265 minutes and can be statistically tested. An appropriate Null Hypothesis is that behaviour of one bird is not influenced by the activity of the other. Observed activities can be tabulated in minutes under the categories 'both feeding', 'one feeding/one perched' and 'both perched' and expected values for these cells can be calculated. A chi-squared analysis of these data yields a highly significant result (P .0001), firmly rejecting the Null Hypothesis of independent behaviour on the part of each bird.

Sentinel birds do not always give an audible alarm call at the approach of danger and vocalizing probably depends on the nature of the perceived threat. As aforementioned, alarms are not normally uttered when a hawk is espied. If approached by a human, a sentinel will sometimes challenge with a strident peeurg call; at other times it will simply fly away. Depending on the intensity of the alarm call, foraging birds may fly up to the nearest elevated perches to see what is coming. Flight on the part of the sentinel invariably results in the rest of the group promptly flushing from their foraging positions and flying off in the same direction. At Wellington, where fence post tops were frequently used as perches (because there were lots of fences and relatively few rocks), a sentinel which saw me walking past on the opposite hillside hitched itself down the far side of its post and gradually sidled around it in order to stay concealed. Perhaps my 'passing-by' distance did not pose an imminent

threat to the woodpecker, but it felt exposed and adopted the same 'keep-out-of-sight' strategy as it would in response to a distantly passing hawk.

DISCUSSION

Of the Ground Woodpecker's three distinctive calls, the peeurg call is the most variable one and appears to serve several functions. In the form of an alarm call, the higher frequencies are emphasised, doubtless ensuring that it is audible above the low frequency, wind-generated noises characteristic of its environment. Similar calls by the Redwinged Starling and the Rock Hyrax suggest that the physical constraints of the environment have resulted in a degree of convergence in the vocalizations of these unrelated species. In this context it is noteworthy that the Northern Flicker Colaptes auratus of North America, which in some areas frequents habitat similar to that favoured by the Ground Woodpecker, has an almost identical call (I.A.W. Macdonald, pers. comm.).

The erratic peeurg flight is presumed to be a display because it frequently culminates in the spread-wing 'kingfisher' display which usually precedes successful copulation, but Kilham (1974), who has described similar erratic flights in seven species of nearctic woodpeckers, considers them to be forms of play; he notes that they usually occur within the first hour of daylight and involve dodging amongst trees. Whether or not Kilham's interpretation is valid, it is evident that there is a propensity for such a flight form in picids. Short (1982) refers to "flutter flights" and comments that they often culminate on landing with a spread-wing display. Flutter flight displays are generally short flights designed to maximise conspicuousness in the limited field of view in woodland habitats. By contrast, the long, rapid, jinking flight by the Ground Woodpecker takes advantage of the unlimited space and visibility of the open country it inhabits. Further, I have never observed these flights in the first hour of daylight but always in the forenoon or early afternoon; the flight is often performed in front of a resting group.

The erect stance and spread-wing posture of the 'kingfisher' display brings into prominence the red belly feathers and also the contrasting golden-coloured undershafts of the flight feathers. The submissive turning-away and drooped-wing posture of the responding female shows the red rump patch which is otherwise not deliberately displayed by perched birds. The Ground Woopecker is the only southern African picid with red ventral colouring, and although the extent and intensity of this colouring shows clinal variation (for colour illustration see Earlé 1986) it is nevertheless a distinctive feature in all individuals and is a likely component of the SMRS. The carmine-coloured rump may also comprise a link in the chain of co-adapted stimuli which lead to successful coition; it possibly serves a dual signal function since it is visible in flight to following birds. Short (1982) suggests that rump patches in picids may have significance in this context.

The sequence of movements by the male in achieving coition are characteristic of many woodpeckers, it being usual for him to drop over to the female's left side. Crockett and Hansley (1977) have commented that the resulting side-by-side position is presumably assumed to permit cloacal contact which might be made difficult in the orthodox position by the stiffened rectrices characteristic of picids. Kilham (1974) provides a detailed description of the sequence of movements in the Downy Woodpecker Dendrocopus pubescens:

"Once mounted on the back of the female, the male Downy, like the males of other species of woodpeckers ....falls gradually to the left. During this time his tail is moved under that of the female and at the time of cloacal contact is turned forward to lie along her right side. The male meanwhile holds his balance by spreading both wings. His right wing may lie across the lower back and tail of his mate while his left one rests against the branch where she is perched."

Kilham's comment on the purpose of the male's wing position is of comparative interest. Copulation by Ground

Woodpeckers usually takes place on flat rocks, not on rounded and often narrow branches; balance is consequently not a problem for the male so his right wing does not have to be braced across the female.

The level, head-in-line-with-body, precopulatory pose of the female may be significant in the context of the lack of distinctive crown and nape markings in the Ground Woodpecker. In some woodpeckers with bold head patterns, the female's invitation stance is characterised by her head being held up and tilted backwards (e.g. Great Spotted Woodpecker, Steinfatt 1937; Downy Woodpecker, Lawrence 1967).

In summary, the SMRS of the Ground Woodpecker would seem to comprise a sequence of signals involving the peeurg and wee-chik calls, the precopulatory displays and postures and the unique plumage patterns. The vocalizations and plumage patterns are peculiar to this species and have resulted from its adaptation to its prefered environment, whilst the movements and postures are versions of evidently deep-seated, innate behavioural patterns which became established early in the woodpecker lineage.

One unique behavioural characteristic of woodpeckers, the use of the bill to produce loud drumming sounds on appropriate wooden substrates, needs mention. Drumming is used by arboreal woodpeckers for signalling (Jellis 1977), each species employing unique cadences of beats, and slower tapping may be used in many species as a form of signalling between members of a pair, especially during reproductive activities (e.g. nest relief). It is not surprising that birds adapted to chiselling holes into hard wood to obtain food and shelter for themselves and their young should have developed the acoustic byproduct of such activity into species-specific signals in sylvan habitats where limited visibility favours acoustic display. It is equally unremarkable that a terrestrial woodpecker adapted to a virtually treeless habitat with unlimited visibility should have lost both the means and the need for such signalling.

Sullivan (1984) discusses social foraging in the Downy Woodpecker and shows how the woodpeckers benefit from membership of mixed species flocks through the enhanced vigilance of such groups. Mixed flocks of birds are a common feature of woodlands and forests in both temperate and tropical regions worldwide. In Africa, such flocks frequently include a pair of woodpeckers. Members of mixed flocks may enjoy enhanced foraging success directly through the collective 'beating' action of the flock and indirectly through group vigilance releasing extra time for individual foraging. Woodpeckers have comparatively specialized feeding techniques and are unlikely to benefit directly from the flushing of cryptic prey by other flock members so the advantage of joining such bird parties must stem largely from the benefits of group vigilance. My own observations of bird parties (Oatley 1969) lead me to believe that for the majority of flock members, early warning of approach or attack by a predator is of greater benefit than enhanced foraging opportunities.

The Ground Woodpecker makes no recourse to joining such mixed species flocks which are essentially phenomena of sylvan habitats. They have instead taken collective vigilance to a level not achieved by any other picid by developing a sentinel system. Because the sentinel does not often use vocal warnings but is always perched close to the foraging mate or group, it is evident that the look-out, in addition to being vigilant, must be visible to those of its group foraging on the ground so that its actions cue the foragers to appropriate responses. A foraging woodpecker will be looking for ant nest holes but it can look up at intervals to see the sentinel, who is probably in the periphery of its vision most of the time. A feeding bird necessarily has its head down, beaktip in the ground and tongue at work extracting ants from their subterranean galleries, but at such moments it does not need to look at the ground and can conceivably keep the sentinel in view.

Sentinels orientate to the sun, if it is visible, in the same way as resting birds do. The function of such

deliberate orientation is debatable; its possible role in thermoregulation has been discussed in Chapter 3. In the context of vigilance it could be beneficial for a different reason. If it is advantageous for a predator to mount an attack with the sun behind it, then by facing the sun the prey could ensure that it was scanning the direction from which danger was most likely to come. It is not possible to do more than speculate on this matter since actual attacks on Ground Woodpeckers have not been observed, except for the incident involving the Rock Kestrel mentioned earlier in this chapter, but a light overcast prevailed at that time. Quantitative evidence would be hard to gather and it might be expected that wind direction and speed could also influence the angle and direction of attack by a bird of prey. The fact that Ground Woodpecker sentinels will perch with their backs to relatively strong winds in order to face the sun does not provide much support for the concept of thermoregulatory benefit, but such orientation would enhance vigilance if hawks or falcons frequently attack 'out of the sun' as fighter pilots did in World War II. Whatever the explanation, it seems evident that risk of predation has been, and possibly still is, an important component of the Ground Woodpecker's environment.

o o O o o

6. BREEDING BIOLOGY AND GROUP SIZE

"Though belonging to the woodpecker tribes, it never pecks wood, but bores its way into the banks of rivers, sides of hills, or the walls of mud buildings, in search of its prey, and for a home for its young.
It excavates a hole, sometimes several feet in depth, in which to deposit its eggs, which are pure white and from three to five in number."

Edgar Leopold Layard (1867): The birds of South Africa.

INTRODUCTION

Knowledge of the breeding biology of the Ground Woodpecker is relatively elementary. The known facts relate to the time of nesting, the nest sites, clutch size, egg dimensions and the role of the sexes in the incubation and feeding of the young. The incubation and nestling periods have not been determined. The lack of information on breeding is undoubtedly due in part to the relative inaccessibility of the nest chamber which precludes inspection of the contents without special equipment.

TUNNEL EXCAVATION

The excavation of the nest tunnel would logically qualify as the first step in the breeding cycle. Tunnels are utilized for both nesting and roosting however, and may be occupied throughout the year. They also appear to be fairly durable, so a popular site (Fig. 13) may have many tunnels and there is not always the need for new excavations at the beginning of each breeding season.

There are two published references to tunnel excavation by Ground Woodpeckers. In the first (Robinson et al., 1957) two birds were observed excavating a tunnel in May. It was noted that the work was 'leisurely' and after two consecutive daily measurings it was found to have increased in length by 5 cm. The month of May is well outside the breeding season so conceivably the tunnel was to serve as



Figure 13. Tunnels of Ground Woodpeckers in the bank of the dam at Wellington, Natal. The bank also contained tunnels of smaller birds such as sand martins; the woodpecker's favoured holes are indicated by arrows.

a roost.

The second published report is by Short (1971d) who observed tunnel excavation near Dullstroom, Transvaal, in September. This was presumed to be a nesting site and was excavated primarily by the male.

The only occasion when I have observed apparent excavation was in May at the Castledene study site, in Natal. The woodpecker appeared to be tunnelling at the top of a bank just under the lip of an overhang and it spent some fifteen minutes on this activity whilst another bird looked on from a nearby outcropping rock face. This took place in warm, sunny weather shortly after midday.

It is probably safe to assume that tunnelling activities that take place outside of the months July to November (the usual breeding season) are for the purpose of roost sites rather than nest sites. Both roost tunnels and nesting tunnels may occur singly or in groups in favoured banks.

NEST TUNNEL SITES

Earthen banks of streams, dry gullies (dongas) or man-made cuttings are the most usual sites for nest tunnels probably because vertical, excavatable substrates occur most frequently in this form in Ground Woodpecker habitats. Slip scars (crescent-shaped banks resulting from soil slumping on steep slopes) are frequently used in the Drakensberg foothills. Weathered limestone cliffs and soft sandstone cliffs have been cited as tunnel sites in publications (Uys and Macleod 1967; Robinson et al. 1957). Other sites, recorded in the Nest Record Card collection of the Southern African Ornithological Society, include a termite mound near Citrusdal in the western Cape, and the chimney of a deserted farmhouse in the Clocolan district of the Orange Free State; both parents were observed feeding two young birds which had emerged from, and were sitting on top of, the chimney. Uys and Macleod (1967), in a paper on the birds of the De Hoop Vlei near Bredasdorp in the Cape, state that the Ground Woodpeckers "show a preference for old ruins, of which there are several in the area, where

they excavate nest holes in the crumbling walls." In this respect the African Ground Woodpecker shows similar behaviour to the Andean Woodpecker Colaptes rupicola, which pockmarks the walls of old buildings with tunnels. There is also an unpublished report of a nest in the Giants Castle Game Reserve in Natal in which the eggs were merely placed in a deep crevice in a large boulder (P. le S. Milstein, pers comm.).

The height above ground level of the tunnel entrance is variable, ranging from 30 cm to over 6 m, and appears to result from the nature of the site chosen, rather than to be a criterion determining choice of site.

The diameter of a tunnel is 75-80 mm with an enlarged chamber at the end. The chamber is seldom in a straight line with the entrance but is offset to one side of the line of the tunnel, or the tunnel is curved. Tunnel length is variable, ranging from 46 cm to 1.07 m in nest records for which dimensions are provided; the length of the tunnel may on occasion be constrained by the nature of the site.

Two nest record cards provide evidence that the same tunnel may be used for nesting in successive seasons. Both records came from the southwestern Cape; in one instance the site was used in two successive years whilst in the other it was stated to be the fifth year in which the birds had bred in the tunnel described.

ALLEDGED USE OF NESTING MATERIAL

The majority of records make no mention of nesting material in the chamber. On three cards it is explicitly stated that the chamber contained no lining whilst in two cards a pad of dry grass is recorded. Both of the latter records are from the Balgowan area of Natal. Ground Woodpeckers sometimes nest alongside Pied Starlings Spreo bicolor which also excavate tunnels in vertical banks and habitually place a pad of grass, leaves and other vegetable material in their chambers. One of the two so-called Ground Woodpecker nests was in April, an improbable nesting date for Geocolaptes but within the range of breeding

dates recorded for the Pied Starling. Neither of the cards records the colour or dimensions of the three eggs noted as being present in each case. However, both clutches reputedly from these nests are listed by James (1970) and are indisputably genuine Ground Woodpeckers' eggs. Given this evidence, an explanation might be that the Ground Woopeckers utilized tunnels previously used as nest sites by Pied Starlings. Notwithstanding these records, the usual situation is for Ground Woodpecker nest chambers to be unlined. In this context it may be noted that nowhere in the world is any species of woodpecker known to gather any form of extraneous material with which to line the floor of the nest chamber (Short 1982).

EGGS

The eggs of the Ground Woodpecker, like those of all other woodpeckers, are pure white; according to James (1970) they are highly glossed. The mean of eleven recorded egg measurements is 28.3 mm x 21.4 mm with a range of 27.4 - 29.5 x 20.1 - 22.7 mm. Recorded clutch sizes from all sources are: 1,(4); 2,(4); 3,(11) and 4,(4). Although Layard (1867), Stark and Sclater (1903) and subsequent standard reference works cite 5 eggs as the upper limit of clutch size I can find no detailed records of five-egg clutches.

TABLE 11. Months in which egg laying is commenced by the Ground Woodpecker.

MONTH	JUL	AUG	SEP	OCT	NOV	DEC
No. of clutches commenced	1	11	8	6	7	3
Percentage of all clutches	2.8	30.6	22.2	16.7	19.4	8.3

Eggs are recorded in the months July to December (Table 11). A clutch of four eggs from the Newcastle area of Natal, dated 2 August 1881, indicates a laying date in late July. This is the earliest date; the latest is for a clutch of three eggs taken at Balgowan in April. For reasons mentioned above this clutch may be suspect and is not included in Table 11.

INCUBATION

Both adults share the task of incubation. Short (1971d) has described activities at a nest with eggs in an advanced stage of incubation. On the basis of three morning observation periods he determined that incubating birds sat for "from one half-hour to two or more hours." Sometimes the male sat for the longer periods and sometimes it was the female. The incubating bird would occasionally emerge from the tunnel and utter peeurg and weechick calls whilst perched on a nearby rock.

One changeover in incubation which I observed at Kamberg in Natal was characterised by similar behaviour, the emergent bird calling loudly from a lofty boulder and another bird responding from a distance, then flying to perch nearby on a lower boulder before flying to the nest hole which was situated only 0.5 m above ground level in the vertical face of a slip scar.

The length of the incubation period has not been determined but is probably in the region of 16 days.

PARENTAL CARE AND FLEDGLING BEHAVIOUR

There are no published records of parental care of nestlings and fledglings by the Ground Woodpecker. My own observations on the feeding of nestlings are limited to a 112-minute spell of observation of a nest hole at Carlisle, Dargle, in September 1979, this being the only nest with young that I have found. The observations extended from 15h33 to 17h25. During this period a total of three visits were made to the brood. The first was at 15h42 by a single bird which spent 14 minutes in the nest tunnel; the next visit was at 16h57, a second adult arrived two

minutes after the first and also entered the nest. Both birds stayed for three minutes so there was a period of one minute when both birds were in the nest tunnel or chamber simultaneously. Both birds paused at the entrance to the nest tunnel for up to a minute before entering, and also for similar periods when leaving, squatting in the entrance and looking out before flying off directly without perching on any nearby rocks.

Parent birds arriving at the nest are not visibly carrying prey items and so must regurgitate food to the nestlings. This can be seen to be the case once the young have left the nest. Adults seen leaving the Dargle nest were not carrying faecal sacs. There is no published information concerning Ground Woodpecker nest sanitation, but the behaviour of a hand-reared bird was very significant in this regard. The bird slept in an inverted polystyrene box with an opening at one side, which roughly approximated the nest chamber. During the day the bird would defaecate anywhere in or around its wire mesh cage, but never in the sleeping box (which was called the 'White House'). Asked about the bird's nocturnal behaviour, Mrs. I. Starck, who had reared the bird, explained: "He goes into his little white house, and I put tissues in there, and when he does his business he pushes the tissues to the front and then sort of does it on the tissues and then sort of wraps it." Such behaviour suggests that feathered nestlings do not defaecate in the nest chamber but perhaps in loose material at the entrance to the chamber.

Fledglings are vociferous, giving vent to gutteral peeurg calls at frequent intervals. For the first few weeks they seem seldom to accompany the foraging parents but tend rather to seek concealment by squatting on low rocks, from where the peeurg call is uttered incessantly to function as a location call. The returning parent usually perches on the highest local point, and the juvenile flies up to join it, begging vociferously but not fluttering or shivering its wings as many young passerines do. It pecks at the side of the adult's bill, the adult gapes and the juvenile puts its beak inside the adult's

beak, much in the manner of young doves.

A recently fledged juvenile, watched in Glencairn, squatted on a convoluted boulder screened by tall grass tussocks and shrubs on the hillside slope above the houses. It made no attempt to orientate to the sun but faced downslope, which placed it at right angles to the sun. Its location was discovered at 15h00, but prior to this and for the ensuing twenty minutes, it uttered guttural purggg notes interspersed occasionally with wee-chick calls. The intervals between calls varied from two to six seconds. At about 16h00 some wee-chick calls were heard from the marsh where the adult was foraging. The juvenile immediately increased the tempo of its purggg calls to one every 1½-2 seconds. The adult arrived at the roofridge of the nearest house to be joined immediately by the vociferously begging juvenile. However, the adult kept its beak high, out of reach of the juvenile, perhaps wary of the close proximity of people on the balcony of the house, and it flew off up the valley, closely followed by the young bird.

Subsequent search located the woodpeckers (now two adults and one juvenile) in dense Hakea growth on the hillside. Because of the density of the vegetation I was able to get close enough to see and hear the adults tapping at dead branches and checking under loose bark for ants. The young bird watched the adults but did not forage itself; it uttered insistent and incessant purggg notes, whilst the adults uttered higher-pitched peeu calls. These did not appear to indicate alarm since the birds were not aware of my presence, but perhaps served to maintain contact in the dense woody vegetation.

When, as is initially often the case, there are two or three fledglings, they stay in fairly close proximity to each other, if not actually sharing the same rock to perch on. If one bird becomes separated from the other two for any reason it will soon fly to join them. The parents habitually forage within a radius of a few hundred metres of the young birds; a move to a more distant site results in the whole group moving, often in follow-my-leader

fashion.

As the young birds get older, they tend to accompany the adults more frequently and remain close to a foraging parent. A group of five kept under observation for 90 minutes in the Cape of Good Hope Nature Reserve consisted of two adults and three juveniles. They were foraging on the ground along surface cracks in outcropping sandstone in an area where the vegetation had been burnt off. During the 1½-hour period from 09h00, an adult fed a juvenile on two occasions; it was not possible to determine whether the same juvenile was fed each time (M.B. Skead, pers. comm.).

Fledglings soon start to investigate crevices, cracks or small holes in any substrate; the tendency to peck at and probe with the tongue any crack or hole appears to be innate and has been mentioned in Chapter 4. The young are actively feeding themselves, albeit still in close association with a parent, about three weeks after leaving the nest.

Short (1971d) found no signs in the specimens of Ground Woodpeckers he collected, of a distended oesophagus, which might reasonably be expected in a species which feeds its young by regurgitation. In the specimens examined, however, the proventriculus was usually enlarged and attained dimensions of 4 x 2 cm. It is evident from this that the Ground Woodpecker can deliver by regurgitation substantial meals to nestlings or individual fledglings, despite the relatively very small size of the prey items.

The young birds and adults remain together as a family group, at least until the start of the next breeding season, usually in July or August, when the onset of strong territorial behaviour on the part of the adult pair results in other members of the group being driven out of the defended area. The evicted birds may not go very far; the three young of the 1984 brood of the 'Hotel' pair in the Golden Gate Highlands National Park were found in August 1985 to be occupying an area adjacent to that which

fashion.

As the young birds get older, they tend to accompany the adults more frequently and remain close to a foraging parent. A group of five kept under observation for 90 minutes in the Cape of Good Hope Nature Reserve consisted of two adults and three juveniles. They were foraging on the ground along surface cracks in outcropping sandstone in an area where the vegetation had been burnt off. During the 1½-hour period from 09h00, an adult fed a juvenile on two occasions; it was not possible to determine whether the same juvenile was fed each time (M.B. Skead, pers. comm.).

Fledglings soon start to investigate crevices, cracks or small holes in any substrate; the tendency to peck at and probe with the tongue any crack or hole appears to be innate and has been mentioned in Chapter 4. The young are actively feeding themselves, albeit still in close association with a parent, about three weeks after leaving the nest.

Short (1971d) found no signs in the specimens of Ground Woodpeckers he collected, of a distended oesophagus, which might reasonably be expected in a species which feeds its young by regurgitation. In the specimens examined, however, the proventriculus was usually enlarged and attained dimensions of 4 x 2 cm. It is evident from this that the Ground Woodpecker can deliver by regurgitation substantial meals to nestlings or individual fledglings, despite the relatively very small size of the prey items.

The young birds and adults remain together as a family group, at least until the start of the next breeding season, usually in July or August, when the onset of strong territorial behaviour on the part of the adult pair results in other members of the group being driven out of the defended area. The evicted birds may not go very far; the three young of the 1984 brood of the 'Hotel' pair in the Golden Gate Highlands National Park were found in August 1985 to be occupying an area adjacent to that which

they had frequented with the adults for the previous several months.

ALLEDGED COMMUNAL BREEDING

Short (1971b) states of the Ground Woodpecker that: "They nest in groups of several pairs, or in solitary pairs which may have a third "helper" associated at the nest."This implies that the Ground Woodpecker can be added to the list of species which are communal breeders. A similar statement is made in his definitive work Woodpeckers of the World (Short, 1982) on page 25, whilst in the species account on page 206 he is somewhat more cautious, stating: "Occasionally one of the young birds may remain with the adults into the next breeding season, perhaps helping to feed their young of that season." It is clear from his paper on the habits of southern African woodpeckers (Short, 1971d) that he observed a trio of birds that foraged together in the afternoons but in the mornings he saw only the mated pair, the male of which was engaged in nest tunnel excavation. He evidently did not see the third bird actually helping at the nest. I can find no other published evidence to confirm or support group breeding in Ground Woodpeckers. In fact all the field evidence gathered is to the contrary and supports the statement of Layard (1867): "Families seem to keep in company until the breeding (urge) separates them."

The breakup of family groups with the onset of breeding territoriality appears to occur without exception throughout the Ground Woodpecker's range. An example of typical behaviour was witnessed at Golden Gate where the home range of one group in the Brandwag area includes the Hotel and adjacent car parks. On August 9th, 1985, the male and female were watched attacking their reflections in the Hotel windows and in the hubcaps and rearview wing mirrors of parked cars and buses. This behaviour was already underway at 06h40 and persisted until about 08h00, when both birds flew off and commenced foraging in nearby grassveld. This behaviour, which started in late July, was repeated every morning, starting at first light, and evi-

fashion.

As the young birds get older, they tend to accompany the adults more frequently and remain close to a foraging parent. A group of five kept under observation for 90 minutes in the Cape of Good Hope Nature Reserve consisted of two adults and three juveniles. They were foraging on the ground along surface cracks in outcropping sandstone in an area where the vegetation had been burnt off. During the 1½-hour period from 09h00, an adult fed a juvenile on two occasions; it was not possible to determine whether the same juvenile was fed each time (M.E. Skead, pers. comm.).

Fledglings soon start to investigate crevices, cracks or small holes in any substrate; the tendency to peck at and probe with the tongue any crack or hole appears to be innate and has been mentioned in Chapter 4. The young are actively feeding themselves, albeit still in close association with a parent, about three weeks after leaving the nest.

Short (1971d) found no signs in the specimens of Ground Woodpeckers he collected, of a distended oesophagus, which might reasonably be expected in a species which feeds its young by regurgitation. In the specimens examined, however, the proventriculus was usually enlarged and attained dimensions of 4 x 2 cm. It is evident from this that the Ground Woodpecker can deliver by regurgitation substantial meals to nestlings or individual fledglings, despite the relatively very small size of the prey items.

The young birds and adults remain together as a family group, at least until the start of the next breeding season, usually in July or August, when the onset of strong territorial behaviour on the part of the adult pair results in other members of the group being driven out of the defended area. The evicted birds may not go very far; the three young of the 1984 brood of the 'Hotel' pair in the Golden Gate Highlands National Park were found in August 1985 to be occupying an area adjacent to that which

they had frequented with the adults for the previous several months.

ALLEDGED COMMUNAL BREEDING

Short (1971b) states of the Ground Woodpecker that: "They nest in groups of several pairs, or in solitary pairs which may have a third "helper" associated at the nest."This implies that the Ground Woodpecker can be added to the list of species which are communal breeders. A similar statement is made in his definitive work Woodpeckers of the World (Short, 1982) on page 25, whilst in the species account on page 206 he is somewhat more cautious, stating: "Occasionally one of the young birds may remain with the adults into the next breeding season, perhaps helping to feed their young of that season." It is clear from his paper on the habits of southern African woodpeckers (Short, 1971d) that he observed a trio of birds that foraged together in the afternoons but in the mornings he saw only the mated pair, the male of which was engaged in nest tunnel excavation. He evidently did not see the third bird actually helping at the nest. I can find no other published evidence to confirm or support group breeding in Ground Woodpeckers. In fact all the field evidence gathered is to the contrary and supports the statement of Layard (1867): "Families seem to keep in company until the breeding (urge) separates them."

The breakup of family groups with the onset of breeding territoriality appears to occur without exception throughout the Ground Woodpecker's range. An example of typical behaviour was witnessed at Golden Gate where the home range of one group in the Brandwag area includes the Hotel and adjacent car parks. On August 9th, 1985, the male and female were watched attacking their reflections in the Hotel windows and in the hubcaps and rearview wing mirrors of parked cars and buses. This behaviour was already underway at 06h40 and persisted until about 08h00, when both birds flew off and commenced foraging in nearby grassveld. This behaviour, which started in late July, was repeated every morning, starting at first light, and evi-

dently persisted into the early part of September (C. Kay, in litt.). As aforementioned, this pair's progeny of the previous season had already moved into an adjacent area, whereas a month earlier on 4 July they were still together as a family group foraging around the Hotel and its vicinity.

GROUP SIZE

During the early part of the breeding season it is not unusual to encounter solitary Ground Woodpeckers. These are presumably either the mates of incubating birds or the lone survivors of the previous years brood, now excluded from the territory of the breeding pair. The fate of these young birds is not known, but it is conceivable that they are allowed to rejoin the parents and the new sibs at the end of the breeding season. There is some circumstantial evidence for this in terms of group size. The largest groups I have personally recorded have been of six birds. One of these was at Coleford Nature Reserve in Natal. When first seen in December 1979 the group appeared to contain three juveniles, two adults (the breeding pair) and one apparently subdominant bird that was assumed to have been a survivor from the previous year's brood. This group was still occupying the same area in June 1980, and all six birds were observed to go to roost in the same hole.

The other six-bird group was first encountered in the Elsies Peak study area in January 1985, occupying the area which had supported a group of four in the previous year. Because the breeding pair of this group were known to have reared only two young in the spring of 1984, the additional two birds had to be members of the previous years group. Although the birds were not colour-ringed, one of them was individually distinguishable by virtue of a skew outer tail feather. This persistent and useful marker allowed the group to be identified as well as the individual. The bird was present in the study group in 1984 and 1985 but was not one of the breeding adult pair.

I have heard mention of groups of seven Ground Woodpeckers and one report of "about ten", though in the

latter instance the informer did not appreciate the significance of group size and gave an estimate rather than a count. Stark and Sclater (1903) refer to group size as follows:

"....it is to be seen wandering about in small parties of from six to a dozen birds, except during the breeding season."

This information was repeated in several subsequent texts by other authors. It must be accepted that large groups (of ten or more birds) are possible, but on the basis of current knowledge they must be exceptional. A tally of my own observations, together with those of friends and colleagues and published records is summarised in Table 12. The maximum group size is six birds and the mean group size of 139 groups is 3.05. On a monthly basis, there is a clear trend for maximum group size in the period February to June, followed by a sharp drop during July to October when breeding pairs are the most commonly encountered groups. Group size starts to increase in November with the emergence of fledglings from the nest tunnels. Early (July) and late (Nov - Dec) breeding attempts affect the means for the months concerned. During the breeding season it is sometimes difficult to determine whether a group of, say, three birds is a breeding pair with a juvenile or the non-breeding remnant of a larger group. Prolonged observation is often necessary to determine accurately the number of members of larger groups as an 'extra' bird may be inconspicuous in its foraging or resting position and is only likely to be seen when the group moves off en masse to another area. It is also commonplace, when there are two fledglings, for each of them to pair off with one of the adults; the two pairs may not forage together throughout the day, though they will usually assemble together for rest periods. Casual observations are thus likely to underestimate actual group size.

Group size does not appear to be related to territory size. It is difficult to determine how much of the home range (the area encompassing all sightings of the group)

TABLE 12. MONTHLY VARIATION IN THE SIZE OF GROUND WOODPECKER GROUPS.

GROUP SIZE	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	TOTAL
ONE	2	1						1	1	4	2	1	12
TWO	3	3	1	3	3	3	5	7	11	6	1	2	48
THREE	3	3	2	1	3	2	8	2	5	2	1	2	34
FOUR	3	1	2	5	2	3	2	1	1	1	2		23
FIVE		1	1	1	1	1	2	1	1		1		10
SIX	2	1	2	2	2	2						1	12
No. of groups	13	10	8	12	11	11	17	12	19	13	7	6	139
No. of birds	41	31	33	46	40	41	52	30	47	26	20	17	424
MEAN GROUP SIZE	3.2	3.1	4.1	3.8	3.6	3.7	3.1	2.5	2.5	2.0	2.9	2.8	3.05

can be defined as territory (the defended area). Overt territorial behaviour seems to be restricted to the breeding season, but the response of both adult male and female to contrived situations involving tape-recordings or mounted models at other times of the year suggests that any part of the home range may be defended at any time if an intruding conspecific is encountered. The extent of the defended area probably bears an inverse relationship to the local population density, so that where the probability of encountering another group is high, the territory size may be comparatively small. Rough approximations of the areas habitually occupied by Ground Woodpeckers range from 21 ha to 70 ha. In the case of the Elsies Peak group (four birds in 1984, six birds in 1985) the area they frequented from January to June was about 35 ha in extent, but the overall range of the group was about 250 ha.

There must obviously be an upper limit to the size of an area that can be effectively defended. The question that must also be addressed concerns the need for defence. Resources of the type usually considered to be limiting, such as food and a place to nest, seem not to be in proximate short supply for Ground Woodpeckers. The adults' awareness of places to feed, rest, hide and sleep in their living area is advantageous, and enhances their prospects of survival and of reproductive success. Ultimately, territorial behaviour must be related to reproductive activity.

The eviction of subordinate group members from the defended area by the adult pair at the onset of the new breeding season results in displaced birds or groups of birds having to find new living areas where they are not subject to harassment. The most immediate need will be to find a roost tunnel; temporarily they may have to roost in deep rock crevices. It seems likely that evicted birds might initially repair to a remote part of the parent group's home range, with which they must have some familiarity. Alternatively, they may move into an adjacent unoccupied area, as the progeny of the Golden Gate 'Hotel' pair appeared to do. Such non-breeding groups then become

pioneers in the sense of occupying new ground.

This situation bears comparison with new herd formation in an African antelope, the Impala Aepyceros melampus. At the time of rutting, adult males fight for control of the females. Subadult rams, who are no match for the adult males in a contest, form small batchelor groups and move away into unfamiliar areas; on reaching maturity, those rams which succeed in winning females may form new breeding herds in the pioneered area (pers. obs.). Colonisation of unoccupied areas by non-breeding groups can thus lead to range expansion and promote the effective exploitation of natural resources.

As has been shown in Table 12, a group size of three birds is common in Ground Woodpeckers. Such groups are often composed of a breeding pair and one other which is usually an offspring. If the function of group size is the promotion of collective vigilance against predators, then a single bird when evicted from parental territory, should associate with any other evicted conspecific individual or group that it may chance to encounter. Any association formed in this way could give rise to new breeding pairs in subsequent seasons.

SUMMARY

Ground Woodpeckers excavate tunnels in earthen banks for roosting and nesting. Tunnels are 75 - 80 mm in diameter and from 46 cm to over one metre in length with an enlarged chamber at the end. Eggs are laid between late July and December; documented clutches range in size from one to four eggs, with three-egg clutches being the most usual. More than half of the recorded clutches were commenced in August (30.6%) and September (22.2%). The sexes share the task of incubation and parental care of nestlings and fledglings. The young are fed by regurgitation until they start to feed themselves which they may do three weeks after fledging. The adults and young remain together as a family group until the start of the next breeding season. Although Short (1971b) has stated that

there may be a helper at the nest, communal breeding has not been observed. The annual disbanding of parent-progeny groups at the onset of breeding distinguishes the Ground Woodpecker from truly social species. Group size is generally largest between January and July. The largest groups encountered in this study have been of six birds; the mean size of 139 groups observed was three birds. Group siz is not related to territory size. Habitually occupied areas range from 21 to 70 ha; overall home range of one group in the southwestern Cape was 250 ha. Adults may act aggressively towards strange intruding conspecifics throughout the year, and since there are no grounds to invoke food and nesting sites as limiting resources, territorial behaviour probably serves to defend favourable living areas. Colonisation of new areas by non-breeding birds evicted from parental territory may result in range expansion and possibly in the formation of new breeding pairs.

o o o O o o o

7. RELATIONSHIPS OF GEOCOLAPTES

"Genetic storage is a nuance of evolution too often ignored."

Robert Bakker (1986): The Dinosaur Heresies.

INTRODUCTION

Published opinions concerning the relationship of Geocolaptes to other Afrotropical woodpecker genera were mentioned briefly in the Introductory Chapter. These hypotheses will now be examined in more detail.

In the Afrotropical region the subfamily Picinae contains 24 to 26 species according to recent authorities (White, 1965; Goodwin, 1968; Short, 1982). Table 13 lists the genera and species recognised by each; the three arrangements differ primarily in the number of genera recognised, and in the generic status of some species. Goodwin recognises two extra species in Campethera taeniolaema and Dendropicos lugubris which the other two specialists consider to be races of C. tullbergi and D. gabonensis respectively. White's Check List does not explicitly discuss generic relationships but his placing of Geocolaptes at the beginning presumably reflects its supposed primitive status. Short (1980) likewise placed Geocolaptes first, but in his 1982 monograph it follows Campethera. Goodwin considers that the Ground Woodpecker shares a common ancestor with some Mesopicos species (goertae and griseocephalus) and so places Geocolaptes close to that genus.

All but one of the species listed are endemic to Africa and have no congeneric relatives outside of the afrotropical region. The exception is the Brown-backed Woodpecker, obsoletus, which Short now places in the genus Picoides. Goodwin includes it in Dendropicos, as did Bannerman (1953). Mackworth-Praed and Grant (1952) called it

TABLE 13. Recent taxonomic arrangements of Afrotropical woodpeckers.

WHITE (1965)	GOODWIN (1968)	SHORT (1982)
GEOCOLAPTES	CAMPETHERA	CAMPETHERA
olivaceus	bennettii	punctuligera
CAMPETHERA	nubica	bennettii
punctuligera	punctuligera	nubica
nubica	notata	notata
bennettii	abingoni	abingoni
abingoni	cailliautii	maculosa
notata	taenioiaema	cailliautii
maculosa	maculosa	nivosa
cailliautii	tullbergi	tullbergi
caroli	caroli	caroli
nivosa	nivosa	GEOCOLAPTES
tullbergi	DENDROPICOS	olivaceus
DENDROPICOS	fuscescens	DENDROPICOS
fuscescens	stierlingi	fuscescens
stierlingi	elachus	poecilolaemus
elachus	abyssinicus	abyssinicus
abyssinicus	poecilolaemus	elachus
poecilolaemus	gabonensis	gabonensis
gabonensis	lugubris	stierlingi
DENDROCOPOS	obsoletus	namaquus
obsoletus	GEOCOLAPTES	pyrrhogaster
MESOPICOS	olivaceus	xantholophus
goertae	MESOPICOS	elliotii
griseocephalus	goertae	goertae
xantholophus	griseocephalus	griseocephalus
pyrrhogaster	elliotii	PICOIDES
elliotii	THRIPIAS	obsoletus
THRIPIAS	namaquus	
namaquus	pyrrhogaster	
	xantholophus	

Ipophilus obsoletus, whilst Chapin (1939) placed it in Yungipicus and remarked that in the field it reminded him of a small Dryobates (e.g. Picoides pubescens). The genus Dendrocopus, to which it was assigned by Peters (1948) and White (1965) is now generally merged with Picoides. Short (1982) considers the Brown-backed Woodpecker's relationships to be with the 'Pied' Woodpeckers of east and tropical Asia, and believes it to be a 'recent' immigrant to the afrotropical region, probably by way of the Arabian peninsula where its closest relative, Picoides dorae occurs. Thus the majority opinion through the years has regarded the Brown-backed Woodpecker to be related to the cosmopolitan Pied Woodpeckers; this, together with its primarily northern savanna distribution (it only extends south of the equator in a small portion of East Africa) makes it an unlikely candidate for relationship to the Ground Woodpecker.

EXISTING HYPOTHESES

The two published opinions regarding the ancestry of the Ground Woodpecker are set out below in the order in which they were published.

The Goodwin hypothesis.

Goodwin's comments on woodpecker relationships are contained in a 44-page bulletin published in 1968. They arose from an examination and re-arrangement of the material housed at that time in the British Museum of Natural History. Goodwin's field experience of woodpeckers was, at his own admission, limited to the three species occurring in Britain and to brief observations of some other European and Nearctic woodpeckers made during visits to Austria and North America. His conclusions are, in his own words, "based mainly on external morphological characters." He also states that he does not depart from the arrangement in Peter's (1948) Check List except where the evidence favouring such a course appeared to him to be overwhelming.

Goodwin makes significant comment on the criteria used

by Peters (1948); by the use of correlated foot and bill characters it is possible to divide the Picinae into two major groups. He finds that these groupings separate "some "pairs" of genera whose geographical distributions, colour patterns and general similarity suggest close relationships between them" and names Geocolaptes and Mesopicos as one of the examples of such related genera. As a consequence, Goodwin concludes that "bill and foot differences may be rather labile adaptive characters....".

Goodwin discusses sexual dimorphism and provides a comprehensive review of juvenile plumages; in neither of these does Geocolaptes find mention. In the taxonomic section of his paper the African woodpeckers are treated en bloc in a separate subsection because "All the sub-Saharan African woodpeckers seem to be more closely allied to one another than to any non-African species or genus." In this context obsoletus is treated as a species of Dendropicos, as aforementioned. In discussing this genus, Goodwin suggests that on the basis of head markings, Dendropicos species are closer to Thripias and Mesopicos than to Campethera. He considers the resemblance of the African Ground Woopecker to some American Flickers, Colaptes, to result from convergence for similar life styles. He notes the "very close resemblance" between Geocolaptes and Mesopicos goertae and M. griseocephalus in colour pattern (apart from the barred tail pattern of Geocolaptes and the male's vestigial red malar stripes) and suggests that the Ground Woodpecker evolved from some stock ancestral to both itself and these two species.

Goodwin does not discuss parallelism or character convergence, a phenomenom which is considered by some authors, notably Cody (1969), to be particularly well exemplified in woodpeckers and to explain why sympatric species belonging to different genera exhibit striking similarity of colour and plumage pattern. Character convergence is a fashionable theory for those who believe that competition plays an important role in "driving" evolutionary processes. Wiens (1977) and Walter et al. (1984) have drawn attention to the weaknesses of such

reasoning, chief among which is the general inconstancy through time of competition-driven selective pressures which could affect speciation processes. The theory of character convergence warrants mention here because some of the 'generic pairs', which Goodwin considers to be indicative of relationship, would be considered by adherents of competition theory to be examples of character convergence. It should be noted however, that the Geocolaptes - Mesopicos similarity has not been remarked by other authors, and is not one of the classic character convergence examples.

The Short hypothesis.

Dr. Lester Short is indisputably the world's leading authority on woodpeckers. His firsthand field knowledge of every living species of woodpecker is an asset that undoubtedly aids his assessment of their taxonomic relationships. In addition, he has taken a particular interest in the terrestrial woodpeckers and published his theories regarding their evolution (Short 1971a; 1971e).

His hypothesis concerning the relationship of the African Ground Woodpecker is succinctly summarized in a single sentence in his paper on speciation in African Woodpeckers (Short 1980): "It appears to have evolved from some ancestral species of Campethera, with specializations for a ground-living existence."

The basis for this statement has to be sought in earlier publications, particularly in the aforementioned paper on the evolution of terrestrial woodpeckers, in which Short figures a hypothetical evolutionary tree to indicate the relationships of the genera of ground-foraging woodpeckers. The tribe Campetherini is shown branching away from the ancestral stock before either the Colaptini or the Picini. These three tribes include the genera Geocolaptes, Colaptes and Picus, to which the twelve or more ground-foraging woodpeckers belong.

Short believes that all ground-foraging woodpeckers (these include the three fully terrestrial species) are descended from ant-eating ancestors; he also considers

that the ant-eating habit is a preadaptation to a terrestrial existence. In this context it is noteworthy that the terrestrial Andean Flicker, Colaptes rupicola, evidently does not eat ants. Furthermore, since the tribe Campetherini includes the genus Dendropicus plus the other genera Mesopicos and Thripias now merged with it, and Picoides, it follows that these primarily non-formicivorous genera are likewise descended from ant-eating ancestors.

A peculiar trait which Geocolaptes shares with Campethera is the asymmetric lateral extension of the enlarged left testis (Short 1971d).

In summary, it is evident that Short adopts a vertical approach to the arrangement of genera and assessment of relationships, in which presumed ancestral connections are given prominence. Geocolaptes is considered to have arisen early in the ancestral line of the Campetherini from the same stock that gave rise to the genus Campethera; it is also considered to be older than the two South American terrestrial woodpeckers of the genus Colaptes.

The fact that the African Ground Woodpecker is so different in appearance and ecology from other living African woodpeckers requires it to have undergone substantial change, irrespective of its ancestry. If the genus Picoides, which Short (1980; 1982) considers to have descended from ancestral Dendropicos, is excluded, the remaining true woodpeckers of the Afrotropical region fall into two major genera according to Short. These two genera, the ant-eating Campethera and the non-formicivorous Dendropicos, conceivably form two monophyletic groups. There is circumstantial evidence in terms of the above two hypotheses to support relationship of Geocolaptes to either group. An objective of this study has been to find new evidence to resolve this dichotomy of opinion or to identify another relative.

TONGUE MORPHOLOGY

Woodpeckers' tongues form an essential part of their feeding apparatus and are consequently highly specialized

organs. Elongated hyoids permit extension of the basihyal which is also greatly elongated and culminates in a stiffened tip that comprises the entoglossum and its associated epithelium (Campbell and Lack 1985).

Sielmann (1959), refering to the tongues of European woodpeckers, states that there are two types of tongues: sticky tongues and harpoon-type tongues. The latter have sharp tips with reverse-angled spines, enabling wood-boring insect larvae to be impaled and withdrawn from their tunnels. The sticky-type tongue is exemplified by the Green Woodpecker, Picus viridis. This is a ground-foraging woodpecker which has the most specialized feeding ecology of western Palearctic Picinae and subsists largely on adult and pupal ants (Cramp 1985). Its tongue can be extended more than 10 cm and has a unique unbarbed, spoon shaped tip which can be moved independently of the rest of the anterior portion of the tongue (cf. Sielmann 1959, photograph facing p. 113).

There appear to be no published details of the tongue morphology of African woodpeckers. Clancey (in litt) has mentioned that when handling Geocolaptes he had been impressed by the great length of its tongue and the problem presented (to the skinner) by the extreme viscosity of the saliva adhering to it. He had no comment to offer on the shape or nature of the tongue tip.

It seemed possible that tongue morphology, specifically the characteristics of the true tongue (entoglossum), might offer some clue to the relationship of the Ground Woodpecker to other African picids.

Tongues have been examined of the following species and numbers of individuals: Geocolaptes olivaceous, (2); Campethera abingoni, (4); C. bennettii, (1); Dendropicos fuscescens, (3); D. griseocephalus, (5) and D. namaquus, (1).

As expected, species of the genus Dendropicos all have sharp, harpoon-type tongue tips with variable numbers of reverse-angled spines. Tongue tips of the ant-eating Ground Woodpecker and the two Campethera species differed only in having blunt-tipped, as opposed to sharptipped

tongues. In C. abingoni all four specimens examined differed in the degree of bluntness. The number of spines also appeared to be subject to intra-specific variation in all species for which two or more specimens were available.

It is evident that no striking differences in tongue-tip morphology, such as exemplified by the Green Woodpecker of Europe, have evolved in southern African picids, nor, in all probability, in the rest of the African Picinae. Chapin (1939) mentions, in the context of the slow development of tongues of juvenile woodpeckers, that the tongue-tip of a nestling Campethera nivosa had no barbs. He also mentions that the tongue-tip of another member of the Picidae, the ant-eating African Wryneck, Jynx ruficollis, is without barbs. It is unlikely that Chapin would have omitted to mention any unusual tongue morphology in the many species of African woodpeckers which he handled.

It appears therefore, that ant-eating Afrotropical woodpeckers have essentially harpoon-type tongues that are only slightly modified by being blunt-tipped instead of sharp-tipped. This implies that ant-eating genera have descended from non-formicivorous ancestors, contra the aforementioned opinion of Short.

Although the tongue of the African Ground Woodpecker is known to be very long, the length of maximum extension has not been observed. The hyoids reach past the front of the orbits and are inserted into the right nostril. It is the only southern African picid with hyoids of this length; in the other woodpeckers examined, the hyoids do not extend beyond the anterior rims of the orbits. The Ground Woodpecker's tongue is also highly manoeuvreable. Once, whilst watching one of the Wellington Ground Woodpeckers feeding, I saw it lift its head with what appeared to be a wriggling earthworm protruding from its beak. It took me a few seconds to realise that it was the woodpecker's tongue and not some unusual prey item at which I was looking. It is not known how other species of African woodpeckers compare in the matter of tongue flexibility.

THE FOSSIL RECORD

The fossil record for birds in Africa is, as elsewhere, comparatively poor. However, one of the richest avian fossil deposits in the world is located at Langebaanweg, approximately 100 km north of Cape Town, and within the present-day range of the Ground Woodpecker. The site was apparently a freshwater one and has been dated to the Pliocene - Pleistocene boundary some 7 - 3.5 million years B.P. (Hendey 1970).

Rich (1980) provided a relative abundance rating for the different avian orders and families represented, on the basis of tarsometatarsi, the most common skeletal element. Piciformes were ranked lowest, along with several other orders, each contributing less than 1% of the fossil tarsi. There are seven tarsometatarsi (three of which are incomplete) derived from woodpeckers. These have been examined in detail and compared with tarsometatarsi of extant southern African Picinae. The comparative measurements are given in Table 14. It can be seen that none of the fossil tarsometatarsi exceed the dimensions of those of modern Geocolaptes. Two are almost a match in size but differ in the structure of the hypotarsus.

The pre-Pleistocene environment at Langebaanweg is presumed to have been characterised by several depositional phases, including marine shore, pond, marsh and floodplain. The high representation (58% of identified tarsometatarsi) of Francolins (Phasianidae), plus the remains of mousebirds (Coliidae) and parrots (Psittaciformes), each contributing 2%, can be related to a floodplain environment with bush thickets and fringing tree savannah. Many extant woodpecker species may be encountered in habitat frequented by mousebirds and parrots, but with one exception would not be found in marine shore or marsh environments. This exception is the Ground Woodpecker, which forages in the splash zone along rocky shores and in reed habitats (Chapter 2) and nests in soft sandstone cliffs along the southern and western Cape coast (Ch. 5, p. 82). Its absence from the fossil collection based on

TABLE 14. Dimensions of tarsometatarsus of extant barbet, honeyguide, Wryneck and five woodpeckers compared with fossil picid metatarsi from Langebaanweg, Cape. A = maximum trans-cotyla diameter; B = anterior - posterior proximal diameter; A/B = hypotarsus index; Inc. = incomplete. Bracketed figures indicate that the dimension may be effected by apparent wear or damage.

SPECIES	TARSOMETATARSUS DIMENSIONS (mm)			
	Length	A	B	A/B
CAPITONIDAE				
Lybius leucomelas	22.6	3.1	3.1	1.00
INDICATORIDAE				
Indicator indicator	16.5	3.7	3.7	1.00
JYNGINAE				
Jynx ruficollis	20.6	3.9	3.5	1.11
PICINAE				
Dendropicos fuscescens	17.6	3.1	3.2	0.97
Mesopicos griseocephalus	19.0	3.9	3.7	1.05
Campethera abingoni	20.1	4.0	3.7	1.08
Thripias namaquus	20.8	4.4	3.9	1.13
Geocolaptes olivaceus	25.9	5.4	4.7	1.15
FOSSIL PICIDAE				
EE N-U8199	(20.4)	5.0	Inc.	-
PQLZ 8198E	(23.9)	5.1	Inc.	-
PQ-L 25293GR	24.5	5.0	(4.7)	(1.06)
HL PQL 28423	23.2	4.7	4.4	1.07
PQL 28423GR	23.0	4.8	4.2	1.14
PQL 43570	25.1	5.2	In.	-

such depositional environments does suggest that it was not present in the area during what must have been a relatively long period of deposition.

DERIVED CHARACTER STATES

With neither tongue-tip morphology nor the available fossil material providing any clear leads to the relationship of the Ground Woodpecker to other extant African picids, the next recourse was to identify character states which differ between the two presumed monophyletic lineages (Campethera and Dendropicos) but are constant in expression for all member species in each group. The one character that fits this requirement is the colour pattern of the head of the juvenile bird. In the majority of woodpecker species, sexual dimorphism in adult plumages is well-marked and manifested in the plumage pattern of the head. In many species it is usual for the juveniles to develop a plumage pattern resembling either the parental male or female, irrespective of their own sex.

In the genus Campethera the juvenile plumage resembles that of the adult female, with red only on the back of the head, whereas in Dendropicos (sensu Short), adult females have no red markings on the head, but the juveniles do and thus resemble the adult males.

Sexual dimorphism in the Ground Woodpecker consists of no more than the red tipping of the grey feathers of the malar stripe in the male. Consequently the adult male has a dusky reddish malar stripe and the adult female a grey one. In immature birds the malar stripe is greyish but usually indistinct. This implies resemblance of the young to the adult female and supports Short's hypothesis of relationship to Campethera. Short (1982) states that traces of a red nape patch are usually present in the immature bird. This is an equivocal clue because, if it is assumed to recapitulate an ancestral adult plumage, red on the nape could refer to a female Campethera or a male Dendropicos. Some adult birds also have a few scarlet-tipped feathers in the nape, but Short makes no mention of the sex of such birds.

The unequivocal clue was obtained only when I was able to see the hand-reared juvenile Ground Woodpecker mentioned in Chapter 6. At the time of viewing, this bird was adjudged to be no more than 36 days old and had achieved full plumage dimensions. The malar stripe was a striking, dark red, more distinct than in many adult males. The further plumage progression of this bird could not be followed as it was released back into the wild not long after I had seen it. This male plumage characteristic has not previously been noted in juvenile or immature Ground Woodpeckers. However, it is well known that woodpeckers (along with other Piciformes) have comparatively long nestling periods and undergo a complete post-juvenile moult which, in many species, commences before they fledge (Sibley 1957). The red malar feathers of juvenile Ground Woodpeckers could thus be lost before the nestlings leave the burrow.

The adoption, even for a short time, of the adult male plumage by young Ground Woodpeckers clearly allies *Geocolaptes* with the *Dendropicos* group, and red nape traces in immature birds then imply recapitulation of the ancestral male plumage.

It is not immediately evident whether the juvenile plumage patterns which resemble adult sexual markings qualify as primitive (plesiomorph) or derived (apomorph) character states. Given that all the species in one or other of the two genera exhibit the same respective pattern, it may be assumed that they share it with a common ancestor. The identification of other character states which segregate between genera is obviously necessary.

One such character state, mentioned by Short (1971d), is the peculiar shape of the enlarged left testis. Chapin (1939) found this in several *Campethera* species which he handled, but did not observe it in any of the other African genera. He noted, however, that he had also found the condition in flickers of the genus *Colaptes*. The reason for this [illegible] is not known; its manifestation in

some (but not all) genera of two different tribes (Campetherini and Colaptini) suggests either that it is a primitive character or that it has arisen independently. The possession of so distinctive a character by the Ground Woodpecker, together with its ant-eating habit, does lend itself to the parsimonious conclusion that Geocolaptes is related to Campethera.

These conflicting indications of relationship had to be resolved. I started this study with no preconceived ideas about the Ground Woodpecker's phylogeny. No aspect of behaviour provided me with any strong inference that the species was descended from an ancestor in the genus Campethera or Mesopicos. I had not yet seen the young hand-reared Ground Woodpecker and so was unaware of the true nature of the juvenile plumage. My only conviction, after five years of field study, was that the species was not as ancient as the concept of phyletic gradualism might lead one to believe.

In the absence of any clear lead I sought some vestigial plumage pattern in the Ground Woodpecker which might provide some fresh clue to its ancestry. The pattern that provided a new direction was the distinctive barring on its flanks. Some specimens show faint barring on the lower belly (Short 1982) and undertail coverts; such barring is variable in intensity, even among birds from the same area (Earlé 1986). There is only one other woodpecker in southern Africa with barred underparts, the Bearded Woodpecker Thripias namaquus.

The validity of considering the barred underplumage of the Ground Woodpecker as a derived character state was not initially important. It served to identify a potential relative, one that had not before been considered by anyone. With the focus of attention on the Bearded Woodpecker, more character states shared between it and the Ground Woodpecker become evident. These include:

1. Distinctive, differentially-coloured tail feather tips, pink, orange, buff or yellow in Ground Woodpecker, yellow to russet-orange in the Bearded.

2. Close size approximation; the Bearded Woodpecker is the second largest picid in Africa and shows complete overlap in wing length with the Ground Woodpecker, though the latter has a longer tail, tarsus and culmen, and is heavier.

3. Similar tail-moult pattern, in which R_1 is shed last; this trait is shared also with the Olive Woodpecker, Mesopicos griseocephalus.

4. Bright yellow tail feather shafts, with the underside of the tail looking especially yellow (mentioned in respect of Thripias by Clancey, 1964; Short, 1982).

TABLE 15. List of character states used in factor analysis.

1. Adults of both sexes have red plumage on head.
2. Only adult male has red plumage on head.
3. Malar stripe present.
4. Juvenile head plumage resembles that of adult male.
5. Juvenile head plumage resembles that of adult female.
6. Tail shafts golden-yellow in colour.
7. Prominent yellowish undertail aspect.
8. Underparts wholly or partially barred.
9. Underparts plain.
10. Prominent red abdominal feathering (belly patch).
11. Tail feather tips differentially coloured.
12. Tail feather moult sequence $R_2 - R_6, R_1$.
13. Tail barred.
14. Red feathering on rump (rump patch).
15. Enlarged left testis asymmetric.
16. Size small (mean wing length 80 - 99 mm)
17. Size medium (mean wing length 105 - 120 mm).
18. Size large (mean wing length greater than 130 mm).
19. Feeds mainly or entirely on ants.

The yellow tail feather shafts are, of course, a feature shared by all the genera except Mesopicos, but only in Thripias and, to a lesser extent, Geocolaptes, does the underside of the tail appear noticeably yellow.

In total, there are more characters to link Geocolaptes to Thripias than to Campethera. Table 15 lists nineteen character states or traits, including all those which Short cites as evidence for relationship between Geocolaptes and Campethera, as well as others aforementioned which segregate well between species and genera. The occurrence or non-occurrence of these character states in eight species of woodpeckers occurring in southern Africa provides a matrix of 152 datum points.

These eight picids are: Campethera bennettii, C. abingoni, C. notata, C. cailliautii, Geocolaptes olivaceus, Dendropicos fuscescens, Mesopicos griseocephalus and Thripias namaquus. Little is known of the traits or ecology of many of the remaining 16 species (including Picoides obsoletus) and for some there remains dispute over their specific or generic affiliation (e.g. Table 13, p. 98); five of these species have their distribution entirely north, and five mainly (70% or more) north of the equator; five species have essentially tropical equatorial distributions not extending south of 10°S and one, Dendropicos stierlingi, has a restricted distribution spanning no more than seven degrees of latitude and is evidently endemic to Brachystegia woodland (Benson and Irwin 1966). By contrast, Dendropicos fuscescens, Thripias namaquus and Campethera abingoni have the most extensive north-south distributions of all Afrotropical woodpeckers, respectively ranging across 52, 49 and 46 dgrees of latitude. C. cailliautii is a tropical species reaching 25°S in Mocambique, whilst C. notata has possibly the most restricted range of any African woodpecker, spanning only four degrees of latitude in the southern and southeastern Cape and southern Natal. Mesopicos griseocephalus ranges from 34°S to just north of the equator.

Boolean factor analysis (Mickey et al. 1981) was used

to determine the patterns of association amongst variables in the data matrix. The technique transforms variables (species) into binary factor scores and combines numbers of cases (characters) into factors for which loadings are calculated. Binary responses are estimated by multiplying the loadings times the scores. The analysis proceeds in cycles to yield several hierarchical factor levels of relationship among the variables. The total number of discrepancies between the observed and estimated responses provides a useful measure of the strength of association of identified sets of variables.

On the basis of the observed responses to the specific characters the analysis indicates that two sets of variables are similar.

In the first factor (which is fitted to the data that account for the greatest regularity), all four Campethera species are grouped, with a total of three discrepancies out of 76 comparisons between observed and estimated data. These discrepancies all relate to Campethera cailliautii and result from its lack of malar stripe and its size.

In the second factor score, Geocolaptes and Thripias are grouped with no discrepancies in 38 comparisons. However, Geocolaptes also features in factor five, which defines the remaining characters not grouped in earlier factors. These include the red rump, red belly and asymmetric left testis, none of which are known to be manifested by the Bearded Woodpecker.

The fact that no other groupings are indicated by the analysis makes questionable the merging of Thripias and Mesopicos into Dendropicos as advocated by Short (1982).

Factor analysis is a useful mathematical tool which delineates distinct clusters of inter-related data without regard to their nature. The intuitive input must be provided by the researcher through the choice of variables and characters subjected to the analysis. In this regard I have eschewed characters such as bill length and bill shape since these may change in the speciation process due to shifts in selective pressures. The ant-eating habit was included as a character because of Short's conviction of

its pre-adaptive importance in the evolutionary history of terrestrial woodpeckers. I shall endeavour to show, however, that a change of feeding specialization is quite feasible in the speciation process.

Many of the characters chosen are presumed to be firmly entrenched in the relevant gene pools. Such characters may be subject to variable expression or suppression. For example, the golden-yellow colour of the tail feather shafts, characteristic of most woodpeckers of the genus Campethera, is almost totally obscured by black pigment in forest-dwelling species such as C. caroli, though the basic yellow colouration is still visible at the base of the shafts.

Variable phenotypic expression of character states seems to be frequently exemplified in the case of the red colouration of the lower breast and abdomen of some African woodpeckers. This feature is a characteristic of the adults of most or all individuals of two northern races of the Olive Woodpecker Mesopicos griseocephalus, but is very seldom expressed in the nominate race of the species and then only in northern populations. Some 12% of southern African Olive Woodpeckers show scarlet tips to some belly feathers, giving a hint of the suppressed colour. Similar variation in expression of the red belly patch occurs in races of the related Grey Woodpecker, Mesopicos goertae, but in the monotypic Fire-bellied Woodpecker, Mesopicos pyrrhogaster, all birds have the red belly.

As with the Ground Woodpecker, all individuals of the above three Mesopicos species have red rump patches. Some species of Dendropicos also have red rump patches but none have red belly plumage. No species of Campethera have red or partially red feathers on either rump or belly.

There is evidence that in the Ground Woodpecker the red rump and belly patch are subject to the same genetic control. Every (1974) describes a partial albino Ground Woodpecker from Maclear in the eastern Cape as follows:

> "The bird exhibits albinism apart from the usual pink colour of the rump, lower breast and abdomen and all but one of the distal webs of the rectrices."

It seems reasonable to presume that the genetic basis for the red belly and rump pattern of the Ground Woodpecker has been inherited rather than independently evolved. The Bearded Woodpecker does not show this pattern, but it is noteworthy that one of the sixteen skins in the East London Museum collection (specimen No. 11161) has pinkish-orange tips to the upper tail coverts and Clancey (1964) explicitly states that the Bearded Woodpecker's upper tail coverts are tipped with scarlet. This indicates that the genetic determinent for red rump colouration is present in the Bearded Woodpecker genotype.

The presumed absence of the asymmetric left testis in Thripias rests on the fact that it has never been reported. Short (1971d) collected a female Bearded Woodpecker but no male during his field studies of southern African Woodpeckers. Chapin (1939) remarked that he had seen the feature only in the genus Campethera, but it is not clear from his text whether he actually handled a male Bearded Woodpecker in breeding condition. The significance of this feature can best be determined in a cladistic analysis.

PHYLOGENY

Apomorphous character states, as defined by Cracraft (1974), are those derived homologous characters which are shared between a species and a common ancestor. Plesiomorphous states on the other hand, are those inherited from a more distant ancestor and exhibited by all descendant taxa. Examination of the states listed in Table 15 indicate that some are obviously plesiomorphous since they occur in several of the species. Some of these characters may be synapomorphous at higher levels of relationship however, and in a cladistic analysis only one valid synapomorphy is needed to define each nested set in a phylogenetic hypothesis.

Synapomorphies, by definition, must be shared between at least two taxa. On the basis of Goodwin's assertion (quoted on page 99) that Afrotropical woodpeckers seem more closely allied to one another than to any non-African

species or genera, it is instructive to frame a cladistic hypothesis for the African genera of woodpeckers, as Irwin (1985) has done for the African coucals of the genus Centropus. Table 16 lists five characters which are exhibited by two or more of five genera of endemic Afrotropical Picinae (sensu White 1965; Table 13). The criterion for inclusion of characters in Table 16 is that they are present or assumed to be present in all the species of a particular genus. In terms of White's arrangement, Thripias, like Geocolaptes, is a monotypic genus.

A cladistic hypothesis for these five genera is shown in Fig. 14. Short (1982) claims that yellow shaft colour "unites all African woodpeckers (except Picoides obsoletus and Sasia africana)". This is not strictly correct, since the five Mesopicos species (M. goertae, M. griseocephalus, M. pyrrhogaster, M. xantholophus and M. elliotii) all have black tail feather shafts. Elliot's Woodpecker, however, exhibits pale yellow bases to the undersides of the tail shafts, indicating that the black colouration could be a derived character state. In terms of cladistic convention, character A then becomes A' for Mesopicos in Fig. 14.

The hypothetical synapomorphy linking Campethera and Geocolaptes, represented by character E in Table 16, is refuted by characters B, C and D and must therefore be considered a plesiomorphic character.

Thripias and Geocolaptes are interchangeable in the cladogram; aside from this alternative, it is not possible to arrange the genera in any other order unless the characters B, C and D are ignored, or unless they can be shown to be invalid hypotheses of synapomorphy by the discovery of a greater number of intrinsic characters supporting a different arrangement.

The inherent weakness of the cladogram in Fig. 14 is that it is analogous to a closed system; the African woodpeckers are but one branch of the world family of woodpeckers, and even if Goodwin's assertion about their close-knit relationship is correct (and tongue-tip morphology discussed earlier in this chapter is supportive of

TABLE 16. Character representation in Afrotropical woodpecker genera.

CHARACTER	Camp.	Dend.	Meso.	Thri.	Geoc.
A. Tail shafts yellow	+	+	-	+	+
B. Juvenile head plumage resembles adult male	-	+	+	+	+
C. Tail moult sequence: $R_2 - R_6$, R_1	-	-	+	+	+
D. Tail feather-tips differentially coloured	-	-	-	+	+
E. Enlarged left testis asymmetrical	+	-	-	-	+

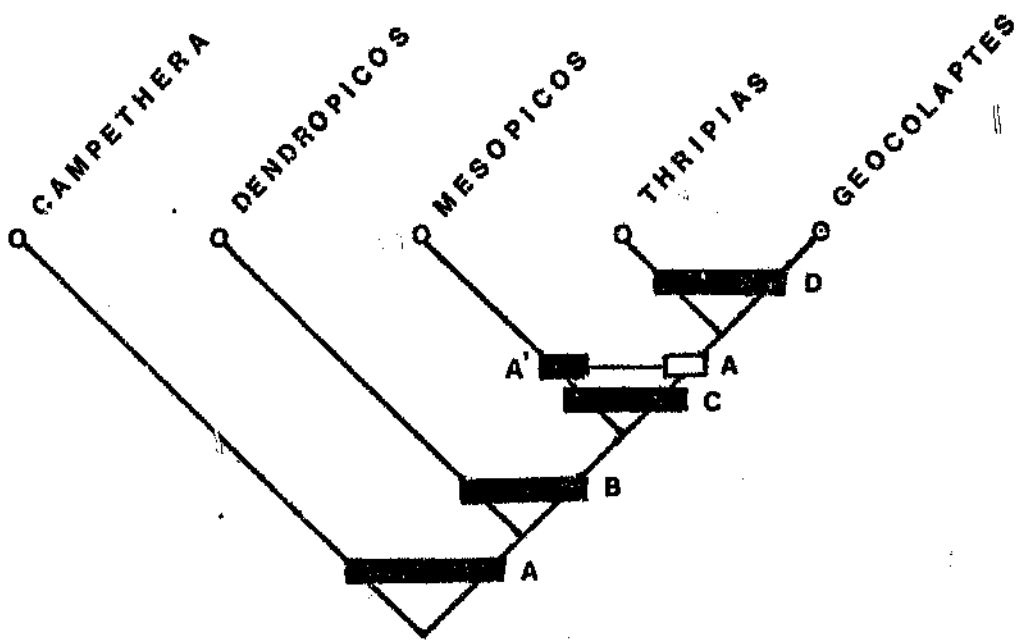

Figure 14. A cladistic hypothesis for five genera of endemic Afrotropical woodpeckers.

TABLE 16B. Character representation used in Outgroup comparison of Afrotropical woodpecker genera with genus Colaptes.

CHARACTER	Col	Cam	Den	Mes	Geo	Thr
Asymmetric left testis	1	1	0	0	1	?
Prominent yellowish undertail aspect	0	0	0	0	1	1
Red rump patch	0	0	1	1	1	1
Red belly patch	0	0	0	1	1	0
Barred underparts	0	0	0	0	1	1
Juvenile head plumage	0	1	2	2	2	2
Tail moult sequence	?	0	0	1	1	1
Tail feather tips	0	0	0	0	1	1
Has Hyonyssus (Gaud & Fain 1989)	0	0	?	?	1	?
Red on head of adult male only	0	0	1	1	1	1

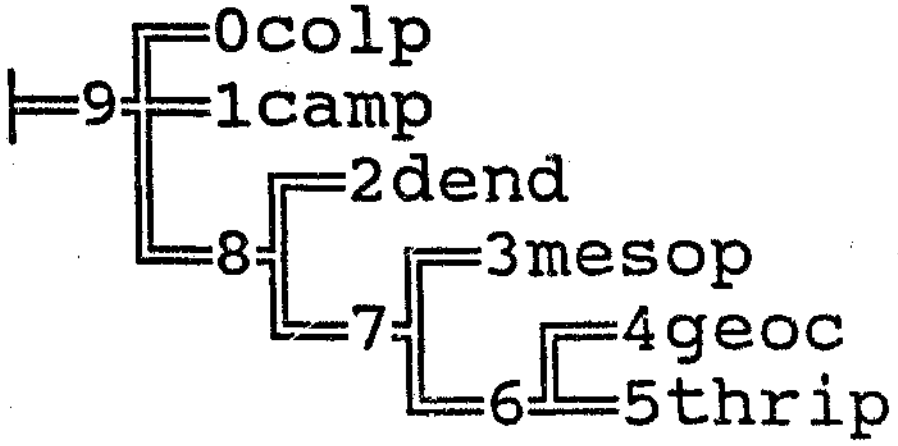

Figure 14A. Outgroup comparison; computer-generated phylogeny of Colaptes and Afrotropical woodpecker genera.

such a view) the only way to test the apparent validity of hypotheses of synapomorphy is by outgroup comparison.

An appropriate genus to employ for this purpose is the American Colaptes. Outgroup comparison is here achieved by use of the Farris 1986 'Hennig' computer program. Table 16A lists the scores for 10 characters (including those listed in Table 16) used in the analysis. Fig. 14A depicts the tree produced. It is notable that this is the only tree the program yields irrespective of the option used. Given that the level of phylogeny being examined comprises genera rather than species (though, as it happens, Thripias and Geocolaptes are each a monotypic genus) and that there are only six genera involved, the problem is a relatively simple one and the single tree result is explicable. It nevertheless provides strong support for the hypothesis that the Bearded Woodpecker and the Ground Woodpecker form a single monophyletic group.

This hypothesis is, to say the least, unexpected and it is likely to be greeted with incredulity by ornithologists familiar with woodpeckers in general and African woodpeckers in particular. It is pertinent therefore to summarise the sundry hypotheses that could or have been proposed to account for the origin of Geocolaptes, and to see what evidence can be mustered in support of each theory.

The following five hypotheses cover the range of possible origins:-

Hypothesis 1. The ancestor of Geocolaptes was an ancient, terrestrial woodpecker precursor or primitive terrestrial anteating form with descendants still extant in South America and southern Africa.

Evidence: Nil.

Comment: Both Colaptes and Geocolaptes are secondarily adapted for a terrestrial existence as adequately demonstrated by Short (1971e).

Hypothesis 2. Geocolaptes is an ancient species derived from an extinct anteating ancestor (Short's hypothesis).

Evidence: Appearance and behaviour are markedly different from all other African woodpeckers; in terms of the concept of phyletic gradualism these differences indicate a long history of evolutionary change.

Comment: The validity of this evidence is totally dependent on validity of the concept and is contradicted by the findings of this study.

Hypothesis 3. Geocolaptes is derived from a Colaptine ancestor that crossed the Atlantic (proposed by Short, 1980).

Evidence: (a) shares asymmetric left testis with Colaptes; (b) two extant terrestrial colaptine species occur in South America.

Comment: (a) Asymmetric left testis also shared with Campethera but other characters do not support an hypothesis of common ancestry with either Colaptes or Campethera; (b) there is no evidence of Andean or Argentinian near-passerines crossing South Atlantic to reach Africa.

Hypothesis 4: Geocolaptes shares a common ancestor with the Mesopicos goertae-griseocephalus superspecies (Goodwin hypothesis).

Evidence: Shares common moult and juvenile plumage patterns; exhibits similarities in adult plumage (especially grey head and red rump) and call pattern.

Comment: There is evident relationship and this hypothesis is not disproved.

Hypothesis 5. Geocolaptes is most closely related to Thripias.

Evidence: Synapomorphic characters shared by these two genera; other circumstantial evidence presented in this study.
Comment: Evidence for this proposal more comprehensive and compelling than for hypotheses 1 - 4.

In summary, it would appear incontravertible that the Ground Woodpecker and the Bearded Woodpecker are more closely related to each other than they are to any other picids in in Africa or elsewhere.

o o o O o o o

8. ANCESTRY AND ORIGIN.

"Selection is a passive consequence of fortuitous interactions between blind variation and blind environments in a supposedly hostile world requiring survival solutions."

Gabriel A. Dover (1988): Evolving the Improbable.

INTRODUCTION

The evidence assembled in Chapter 7 indicates a relationship between the Ground Woodpecker and the Bearded Woodpecker. The far-reaching implications posed by the inclusion of these two species in the same monophyletic taxon will be explored in this chapter.

POTENTIAL ANCESTORS.

Vrba and Eldredge (1984) define a monophyletic taxon as "a group of two or more species descended from a common ancestral species (itself included in the group)." A cladogram sequences taxa according to their common ancestry but does not necessarily imply that ancestors are included in the sample of taxa which it portrays (Eldredge and Cracraft 1980). Many different phylogenetic trees can be derived from the same cladogram, but assumptions have to be made in such procedures.

It is not the purpose of this study to draw up a hypothetical pnylogenetic tree for the Afrotropical woodpeckers. It is relevant, however, to examine closely the different trees that could legitimately provide a true phylogeny for the two species.

For two extant monophyletic species such as these, three hypothetical ancestral relationships are possible:

(1) Both species are derived from an extinct common ancestor.
(2) The Ground Woodpecker is the ancestor of the Bearded Woodpecker.

(3) The Bearded Woodpecker is the ancestor of the Ground Woodpecker.

Most such three-tree problems could not be further resolved but the fact that a major saltation separates the two extant species makes it possible to argue a logical case for the most preferred tree.

Hypothesis 1 satisfies traditional cladistic theory (Hennig 1966; Cracraft 1974) which decrees that ancestors are unknown and unknowable. The hypothesis can take three forms, as depicted by phylogenetic tree diagrams 1(a) - (c) in Figure 15. Since both the Bearded and Ground Woodpeckers are living species, hypotheses 2 and 3 are legitimate alternative assumptions and are depicted by like-numbered trees. However, for reasons of parsimony, the ancestor of Thripias must be assumed to have been a 'normal', arboreal woodpecker, so hypothesis 2 (and tree 2 in Fig. 15) must be rejected.

Tree 1(a), which is a version of the conventional Y-shaped tree representing lineage splitting, implies the contemporaneous initiation of divergence in two separate populations of ancestral species X which, at the same 'instant' of geological time, becomes extinct. An expanded time scale might reveal that these events were sequential, as depicted in 1(b) and 1(c), rather than simultaneous. These two trees differ only in the sequence of origin of Thripias and Geocolaptes.

Hypotheses 1 and 3 are equally possible, but the assumption that both species are derived from an extinct ancestor implies two separate speciation events and an extinction, whereas if it is assumed that Geocolaptes is a daughter species of Thripias, only one speciation event is involved. Parsimony would therefore favour the choice of the third hypothesis (tree 3 in Fig. 15).

As pointed out by and Nelson and Platnick (1981), there is no evidence that evolution is "always, sometimes or even never parsimonious", but if the most parsimonious hypothesis is not prefered there is no basis for favouring

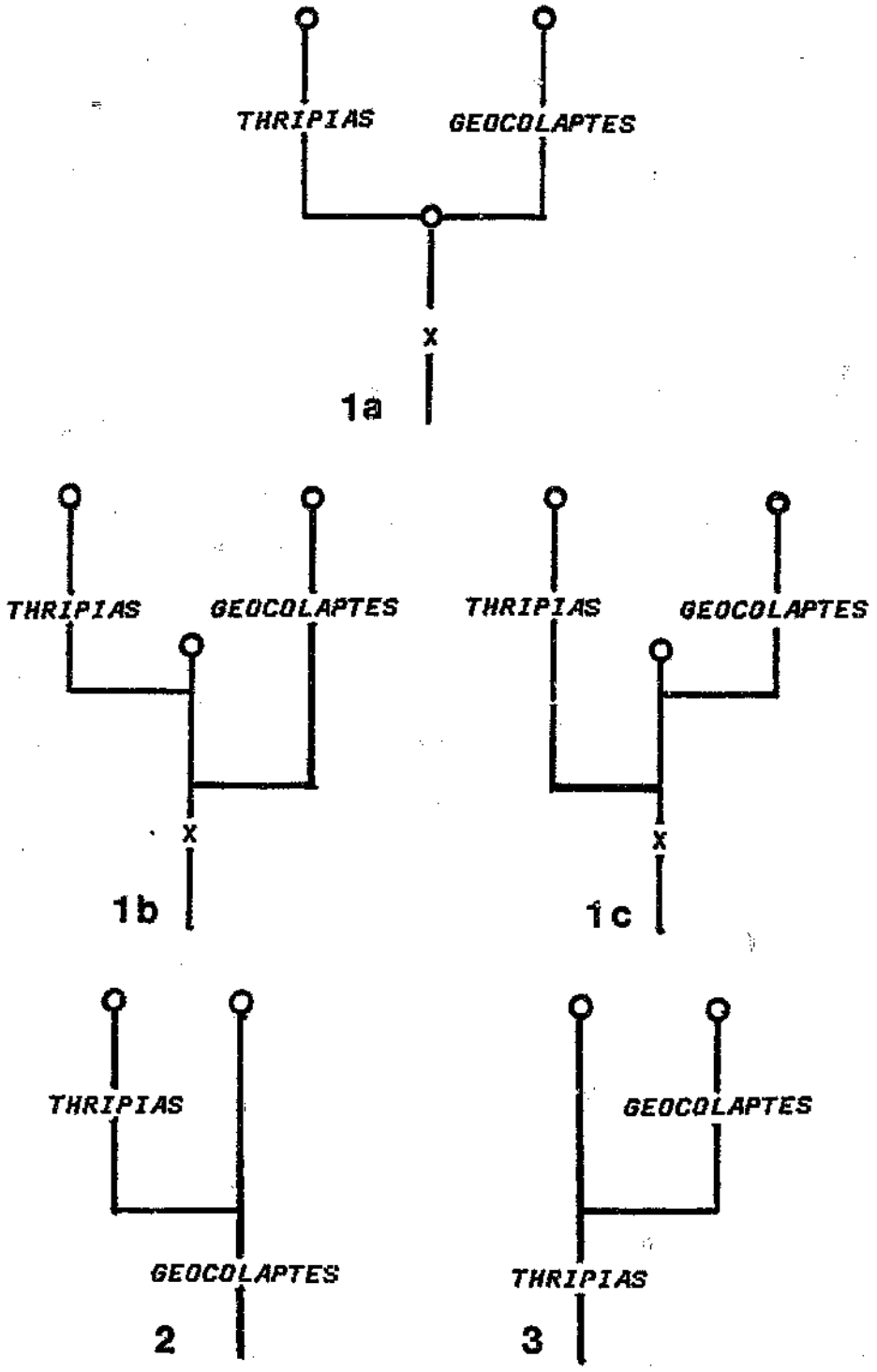

Figure 15. Phylogenetic hypotheses of ancestry of the Bearded and Ground Woodpeckers.

any one of the often numerous alternatives that might explain the observable results of evolution.

If the ancestor of the Ground Woodpecker was in fact the hypothetical extinct ancestor, then, as aforementioned, it must have been an arboreal species, probably not very different from the Bearded Woodpecker. However, the ecological requirements of such an ancestor are perforce unknown, or at best can only be assumed in broad terms. The task of identifying an ecologically plausibly situation embodying the prerequisites for a speciation event (isolation and environmental stress) and is both less speculative and more exacting when the habits and requirements of the ancestor are a matter of record.

OUTLINE OF HABITS AND ECOLOGY OF THE BEARDED WOODPECKER

As with most African woodpeckers, little ecological and biological information on the Bearded Woodpecker has been published. The most comprehensive single account of its breeding biology is by Tarboton (1970). Short (1971d) and Lack (1985) have published accounts of aspects of behaviour and ecology. All three authors have commented that Bearded Woodpeckers prefer areas with large trees. Short (1971d) has stated that the species is more common where large trees are generally distributed and not merely confined to river banks.

Bearded Woodpeckers are usually single or in pairs, not in family groups. Their diet is of wood-boring larvae, caterpillars, spiders, and occasionally lizards or geckos. Clancey (1964) states that the species "feeds on wood-boring beetles and their larvae, as well as ants". Foraging may take place in small as well as large trees, but only on trunks and limbs of the former and never on minor twigs (Short, 1971d). Lack (1985), writing on the comparative foraging habits of three species of woodpecker in Kenya, found the median diameter of branches searched by Bearded Woodpeckers to be 11,4 cm. The bird uses its chisel-tipped beak to expose borer galleries and to chip away loose bark. Bearded Woodpeckers have not been reported foraging at ground level.

Nest holes are preferentially excavated in dead trees and have a distinctive, oval-shaped entrance averaging 75 x 55 mm in height and width respectively. A clutch of two to four eggs is usual; there is no information on incubation period or benaviour. Both parents feed the young, the adult inserting its beak into the open beak of the nestling to relinquish the single prey item brought to the nest.

The species has loud and characteristic vocalizations which have been variously described in different regional texts. Archer and Godman (1961) remark that the call of the Abyssinian race T. n. schoënsis, is like the laughing cry of the European Green Woodpecker, Picus viridis. Short (1971d) studied the species briefly in South Africa and described one call as a long "kwik-wik-wik-wik" and noted that it was similar to the call of the Grey-hooded Kingfisher, Halcyon leucocephala. The most noted aspect of Bearded Woodpecker signalling, however, is its distinctive, slow-paced drumming; this is so characteristic a sound of African woodland that it is imitated, along with the kwik-wik call, by some of the robin-chats, in particular by Ruppell's Robin Cossypha semirufa (North and McChesney 1964).

Throughout its range the Bearded Woodpecker shares its habitat with two or more other picids, the Cardinal Woodpecker Dendropicos fuscescens, and one or more Campethera species. In terms of relative abundance, the Bearded Woodpecker is usually the least common member of such sympatric groups.

MODES OF SPECIATION

The hypothesis of relationship between Bearded and Ground Woodpeckers raises the traditional question of how the latter could be derived from the former and what possible combination of circumstances could have brought about this event.

Paterson (1981) contends that hypothesized modes of speciation can be grouped into two classes on the basis of whether they are or are not supported by observed critical

facts. There is only one Class I model, that of allopatric speciation. Allopatric populations occupy mutually exclusive areas; Mayr (1970) defines allopatric speciation as geographic speciation, though his ideas of the speciation process are not shared by Paterson. In terms of a Class I model, a prerequisite for the origin of the Ground Woodpecker must have been the geographic isolation of a population of Bearded Woodpeckers.

The classic example of a geographically isolated population of a terrestrial species is one confined to an oceanic island. This situation is easily formulated into a mental picture. The isolating barrier is clearly defined and its effectiveness can be ranked in terms of distance. The island is of a finite area and offers grist to the theoreticians mill, both in terms of available space and target size for immigrants. It is not surprising that the island scenario should have been extrapolated to the mainland situation since it is an inescapable fact that the majority of terrestrial speciation events must have taken place on the continental land masses. If the allopatric mode of speciation is espoused as the only acceptable model, then the 'island', or equivalent 'refugium' scenarios, provide the most attractive theoretical options and are regularly invoked.

However, allopatry alone is unlikely to lead to speciation. Refugia, as their name implies, provide island-like pockets of normal or near-normal habitat in extensive, uninhabitable areas. If species maintain their integrity under 'normal' conditions, it is to be expected that they will do the same in refugia, unless further climatic change eventually brings about severe habitat modification in such areas. For significant genetic change to take place the population must be exposed to strong, directional selection pressure, such as may result from a changed environment.

Faced with a changing environment, a population has two options: it may track, if possible, its normal environment by moving to areas with more tolerable conditions, or it may adapt to the new environment. Failure in either of

these responses means that the population will die out. From studies of fossil Coleoptera in the northern hemisphere, Coope (1974) found little evidence of either speciation or extinction during the pleistocene climatic oscillations, and attributed this to the ability of the insects to shift their geographic ranges as the climates changed. Animals which can fly are probably more successful than pedestrian ones in tracking their environment; this much is observable in the present-day migrations of birds and butterflies.

From the above considerations, it follows that the probability of a speciation event will be highest when a population is confined to an area undergoing environmental change. The rate and nature of such change is obviously important, as is the ecology of the animal exposed to the process. It is known that specialized lineages are more likely to give rise to new species than are generalist ones (Eldredge and Cracraft 1980; Vrba 1980, 1984). In this context it is noteworthy that in two different families of birds specialized for life on tree trunks (i.e. Picidae and Sittidae), there are species whose ecology centres on rocks. The African Ground Woodpecker is one such of course, as is the Andean Woodpecker, Colaptes rupicola, and there are two species of Rock Nuthatch, Sitta tephronota and S. neumayer. There is also the Wall Creeper, Tichodroma muraria, now placed in a subfamily of the Sittidae, but previously considered to belong in the Certhiidae (Tree Creepers). Whatever its true systematic status, it seems likely to have been derived from a tree-trunk dwelling ancestor. The switch of affinity from tree trunks to rocks would appear to have been an evolutionary escape route for these species when environmental change deprived them of their normal habitat.

A HYPOTHETICAL SCENARIO FOR THE ORIGIN OF GEOCOLAPTES

Fig. 1 (Ch. 2, p. 12) shows the present range of the Ground Woodpecker lies entirely within southern Africa. It does not approach the Limpopo in the northeast, nor does it reach the Orange River in the northwest Cape Province.

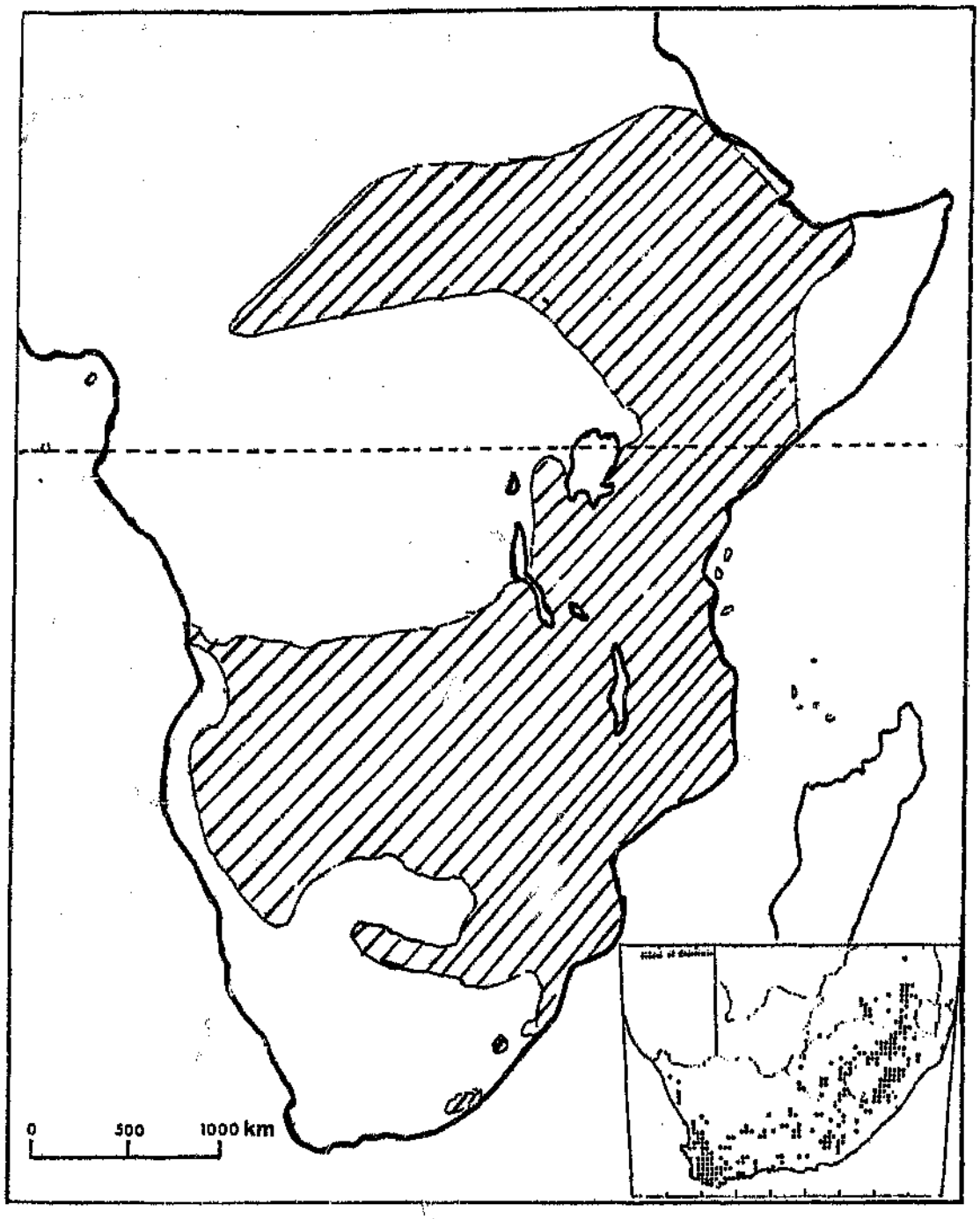

Figure 16. Broad latitudinal range and distribution of the Bearded Woodpecker in Africa. Inset shows distribution of the Ground Woodpecker in the southern Africa.

Present day distributions of animals are not necessarily inclusive of their areas of origin (Coope, 1979). A modern distribution pattern may be relict in nature, a portion of a formerly wider range. When the present range of the Ground Woodpecker is viewed relative to the southern end of the range of the Bearded Woodpecker however (Fig. 16), the two distribution patterns are seen to be largely complementary, and it is reasonable to assume that the Ground Woodpecker originated somewhere within the boundaries of its present-day range.

The logical scenario is for a portion of the Bearded Woodpecker population in prehistoric southern Africa to have become isolated, and for their woodland habitat then to die out totally. However, although it is easy to propose isolation, it is difficult, without invoking numerous ad hoc events, to think of an area in southern Africa in which a population of Bearded Woodpeckers could have been geographically isolated prior to tree disappearance. Alternatively, if it is assumed that the tree die-off brought about the isolation, several possible situations can be suggested. For example, one can propose existence of an extensive area of woodland, of which a portion is persistent whilst the rest dwindles and dies out completely. The persistent portion must subsequently also succumb, perhaps because of increasing severity of environmental factors responsible for the initial diminuation of the woodland.

Paleoenvironmental research in southern Africa has resulted largely in datable periods of the past being labelled as 'warm' or 'cool' or, more usually, 'wet' or 'dry'. Tyson (1986) provides a recent review and summary of our knowledge of past weather patterns, in which the emphasis on moisture regimes is clearly evident.

Short (1971e) advanced the following hypothesis to explain how selection pressures favouring the evolution of terrestrial woodpeckers could have arisen:

"Particular climatic conditions such as the recent increased aridity in many parts of the world caused some

Present day distributions of animals are not necessarily inclusive of their areas of origin (Coope, 1979). A modern distribution pattern may be relict in nature, a portion of a formerly wider range. When the present range of the Ground Woodpecker is viewed relative to the southern end of the range of the Bearded Woodpecker however (Fig. 16), the two distribution patterns are seen to be largely complementary, and it is reasonable to assume that the Ground Woodpecker originated somewhere within the boundaries of its present-day range.

The logical scenario is for a portion of the Bearded Woodpecker population in prehistoric southern Africa to have become isolated, and for their woodland habitat then to die out totally. However, although it is easy to propose isolation, it is difficult, without invoking numerous ad hoc events, to think of an area in southern Africa in which a population of Bearded Woodpeckers could have been geographically isolated prior to tree disappearance. Alternatively, if it is assumed that the tree die-off brought about the isolation, several possible situations can be suggested. For example, one can propose existence of an extensive area of woodland, of which a portion is persistent whilst the rest dwindles and dies out completely. The persistent portion must subsequently also succumb, perhaps because of increasing severity of environmental factors responsible for the initial diminuation of the woodland.

Paleoenvironmental research in southern Africa has resulted largely in datable periods of the past being labelled as 'warm' or 'cool' or, more usually, 'wet' or 'dry'. Tyson (1986) provides a recent review and summary of our knowledge of past weather patterns, in which the emphasis on moisture regimes is clearly evident.

Short (1971e) advanced the following hypothesis to explain how selection pressures favouring the evolution of terrestrial woodpeckers could have arisen.

"Particular climatic conditions such as the recent increased aridity in many parts of the world caused some

constriction of woodlands. Some restricted woodlands, including those containing various ant-eating, largely or entirely arboreal woodpeckers, became savanna-like with trees ever more widely scattered."

The problem that arises when hypothetical changes in vegetation patterns are invoked in terms of changing moisture regimes is that there are no grounds to substantiate such speculation. Dry spells are a natural feature of southern African (and Afrotropical) weather patterns and, as a consequence, much of the natural vegetation is drought resistant and able to withstand the vicissitudes of short-term cycles. Long-term trends are more likely to result in a change in the species composition of woodlands, rather than in their demise, at least until the aridity becomes extreme. The evidence mustered so far is insufficient to warrant assumption of the latter extreme, except in desert regions, such as the Namib.

Altered moisture regimes may be the product of altered temperature regimes since the cooler the atmosphere, the less moisture it can transport. Woodlands tolerant of aridity would perforce retreat if subjected to minimum temperatures of -3°C or lower because of susceptibility to severe frost. Brain (1985) musters cogent support for the notion that the distribution of temperate grassland in southern Africa is determined by the frequency of occurence of subzero temperatures. It is a matter of common experience that mild frosts can kill young trees, and that even mature 'frost-resistant' trees that have survived average winter conditions can succumb to an unusually severe frost (cf. Brain, 1986). In the southern African context then, the advance and retreat of palaeowoodland habitats can be much more plausibly postulated in terms of alternating cycles of relative warmth and severe cold than in terms of moist or dry cycles.

Some aspects of Ground Woodpecker physiology and behaviour indicate that the species probably evolved during a very cold period. For example:

(a) It is less tolerant of warm ambient temperatures than

much smaller birds which share its habitat. An example of this comparative susceptability to heat stress is provided in Chapter 3 (p. 35). Thermoregulation at the upper end of the temperature scale is achieved behaviourally (by seeking shade and bathing) when physiological responses become inadequate.

(b) Though optimally specialized for the capture of termites, which it currently encounters throughout its range, the Ground Woopecker does not normally eat them. Termites, especially their alates, form a nutritious food resource which is exploited by a wide range of animal life from invertebrates to man, including at least five of the 24 species of African woodpeckers. The fact that Ground Woodpeckers don't recognise termites as food (Chapter 4, p. 54) would seem to indicate that these insects were rare or absent from the area in which the woodpecker evolved. The majority of Afrotropical species are found in the tropics, and although there are some primitive, cold-adapted species (including the Black mound termite, Amitermes hasatus, of the southern Cape Province), the characteristic species of the Afrotropical woodlands, the habitat in which termite activity is greatest (Harris 1961), would have retreated with the woodland in the face of intense cold.

(c) The Ground Woodpecker does not glean ants from the surface of the ground. Surface activity of ants is inhibited by very low temperatures, as is the movement of most terrestrial invertebrates. To find food on cold days, woodpeckers would have to locate ant nests. The primarily formicivorous Green Woodpecker of Europe feeds in this way and is known to tunnel through as much as 85 cm of snow in order to reach ant nests (Glutz and Bauer 1980).

(d) The Ground Woodpecker is the largest of Afrotropical Woodpeckers. Although mensurally only some 4-10% larger than the Bearded Woodpecker, its mass is, on average, at least 40% higher. Increase in body mass

can be selectively advantageous in cold-stressed homoiotherms because the altered surface-to-volume ratio reduces heat loss. Size increase might also be favoured for a variety of reasons not directly related to thermoregulation, or even be the result of stochastic processes acting on a small founder population. Nevertheless, size increase is consistent with the hypothesis of speciation under very cold conditions (Bergmann's rule).

In southern Africa there have been several periods within the last 4.5 million years that were not merely cooler than at present, but very cold. Vrba (1985a), using evidence from the fossil record, has shown that some of these cold episodes coincide with periods of lineage turnover in antelope species, and believes that extensive replacement of woodland by grassland must have taken place at these times.

From the foregoing, there are reasonable grounds on which to base the hypothesis that the Ground Woodpecker originated in southern Africa when an ancestral population of Bearded Woodpeckers was stranded in woodland which gave way to open grassland because of a significant depression of minimum temperatures.

Where in southern Africa is this most likely to have happened? The need for the population to have been isolated is a critical factor. The population must also have been large enough to avoid extinction. A recent case history of extinction of a woodpecker population has been recorded in Sweden (Pettersson 1985). A small population (15 - 20 pairs) of Middle Spotted Woodpecker, Picoides medius, was confined by agricultural development to an isolated area of only 300 km^2, situated 500 km from the nearest conspecific population. There was no significant climatic change to bring about extinction. The population remained stable for some 34 years before showing signs of reduced fecundity. Decreasing breeding success brought about extinction in the course of eight years. The site of

this event, at or near the northern limits of the species' range (a fact not mentioned by the author), was conceivably a factor in this case.

There are no published figures referring to population density of Bearded Woodpeckers, but as aformentioned they are generally considered the least common of woodland picids. It must be assumed therefore that several thousand square kilometres of woodland must have been involved in the speciation scenario. Tall tree woodland of the type favoured by Bearded Woodpeckers is today found mainly in tropical and subtropical areas. In warm episodes, which are known to have preceded some of the very cold phases (Tyson 1986), such woodland is likely to have covered much of the area that today forms the Orange Free State (OFS), and would have had a broad connection with the north via land of similar altitude extending through what is today eastern Botswana.

For a variety of reasons, this central plateau area, lying at 1 200 - 1 500-m altitude, is a likely place for the origin of the Ground Woodpecker. The area is in excess of 110 000 km^2. It is bounded to the southeast by the mountains of Lesotho, reaching heights of 3 000 m, the highest peaks in southern Africa. To the north and northeast the land slopes up to the highveld of the Transvaal at altitudes of 1 800 m. To the southwest it merges into the dry plains of the Karoo. The east-west gradient of decreasing moisture which is a feature of the subcontinent today has evidently persisted since at least the early Pliocene (Tyson 1986), so for the past four million years the Karoo is likely always to have been too dry to support the sort of well-developed woodland which constitutes the normal habitat of the Bearded Woodpecker.

The rate, on the ecological time-scale, at which a past warm climate gave way to a cooler one is not known. Tyson (1986) has pointed out that in terms of existing atmospheric circulation patterns affecting the subcontinent, the onset of a cool episode would probably have been characterized by an expansion of the winter rainfall

regime into what is now the summer rainfall area, and need not have resulted in a lowering of annual precipitation levels.

The response of woody vegetation to a changing moisture budget (a product of the nature and timing of precipitation, frequency of cloud cover and wind, and maximum temperature) is likely to have been slow. But winter rains are usually associated with cyclonic depressions; the cold air brought by these fronts is chilled further by adiabatic cooling (6.4°C per 1 000 m) as it sweeps in over the elevated interior of the subcontinent, bringing snow to mountain peaks and high plateaux. Once the cloud cover has dispersed and radiation is unchecked, heavy frosts can occur.

For suitable woodland to have covered much of the OFS, the mean minimum temperatures prevailing there during warm episodes would probably have been at least 3°C higher than at present. Several forms of evidence indicate that during past cold episodes mean minimum temperatures were some 5-10°C lower than at present. Whatever the rate of change of the thermal climate in transition from warm to cold phases, the denudation of woodland would have occured early in the cycle as the normal tracks of cold fronts shifted northward and severe frosts occured with increasing frequency on interior plateaux.

Death of trees from frosting over wide areas would have resulted in the following distinct stages of habitat change:

Stage 1 would involve leaf fall from increasing numbers of frost-killed trees. For woodpeckers this would mean a partial loss of cover. The trees would remain standing however, and the rapid increase in the amount of dead wood would probably prove attractive to Bearded Woodpeckers in the short term. (Clancey 1971, has commented that Bearded Woodpeckers are "particularly plentiful" where dead trees have been left standing in newly logged areas of woodland.)

Stage 2 would be characterised by the progressive

collapse of dead trees; it might be accelerated by high winds and, perhaps, natural fires, though the effects of the latter would likely be localised. For woodpeckers, especially large ones like Bearded Woodpeckers, this phase would mark the beginning of a period of severe stress. Standing trees would become fewer and fewer and it is likely that the woodpeckers would move about in search of more trees.

If the initial die-off of trees was simultaneous over a sufficiently large area, it is likely that the ultimate collapse of the trees would also have occurred over a relatively short period. This factor could have been important in isolating a population of woodpeckers because too slow a deterioration in habitat would induce and enable populations to vacate an area that was becoming intolerable.

Arboreal woodpeckers normally roost in holes in trees. Deprived of its roost by collapse of a branch or tree, an individual bird would need to find an alternative roost quickly or sleep out, since it is unlikely to be able to excavate a new hole in the time available. Under such circumstances any hole provides a refuge, and the woodpeckers would doubtless have done the same as tree-hole roosters do at present when they cannot find an appropriate arboreal roost hole - they take refuge in a hole in a bank. Herholdt and Earlé (1986), have found Pied Barbets Lybius leucomelas and an Ashy Tit, Parus cinerascens, roosting in sandbank tunnels of the Brownthroated Martin, Riparia paludicola. With the fall of trees the Bearded Woodpeckers would also have had to start feeding on the ground, if indeed they had not previously started to do so. Because of their size and weight, they could not easily forage on slender branches of bushes, as the smaller Cardinal Woodpecker does.

The change to terrestrial foraging and roosting would have been inevitable for those Bearded Woodpeckers which could find no end to the frost-devastated woodland. The natural tendency to seek normal habitat would have been

very strong and it is unlikely that similar trains of events in smaller areas could have resulted in the isolation of populations. For example, a belt of land of similar altitude (1 200-1 500 m) can be found to the east in Natal, but because of the steep altitudinal gradient, it is nowhere very wide.

There were possibly only three escape routes from the Orange Free State plateau that would have enabled Bearded Woodpeckers to find normal woodland habitat. The disposition of these routes is depicted diagramatically in Fig. 17. The main route in the northwest would have permitted a withdrawal to warmer woodlands beyond the expanding limits of the cold fronts. The other two would have been southwards and southeastwards around the mountains of Lesotho, down to the basins of the Great Fish and Kei rivers of the eastern Cape and the Tugela River in Natal, where isolated populations of Bearded Woodpeckers currently occur. These southern isolates are appreciably darker underneath than nominate Thripius namaquus and have been described as a separate subspecies T. n. coalescens by Clancey (1958b).

The eastern Cape population is isolated by some 300 km from the population in the upper Tugela basin, which in turn is isolated by some 100 km from the next nearest recorded population in the Umfolozi drainage system in Zululand (Cyrus and Robson 1980). The Umfolozi valley represents a significant zone of discontinuity for many polytypic species of birds, the populations on either side usually belonging to different subspecies. Several bird species which are today common residents in the Orange Free State have disjunct populations in the eastern Cape and northwestern Natal. Notable amongst these are the Blue Korhaan, Eupodotis caerulescens, Titbabbler, Parisoma subcaeruleum and the Red-headed Finch, Amadina erythrocephala; the latter species is a winter visitor to the eastern Cape. An intra-African migrant, the Cliff Swallow, Hirundo spilodera, a breeding summer visitor which is abundant in the OFS, also exhibits similar distribution. This repetitious pattern provides compelling support for the hypothesis that the two Bearded Woodpecker populations in the

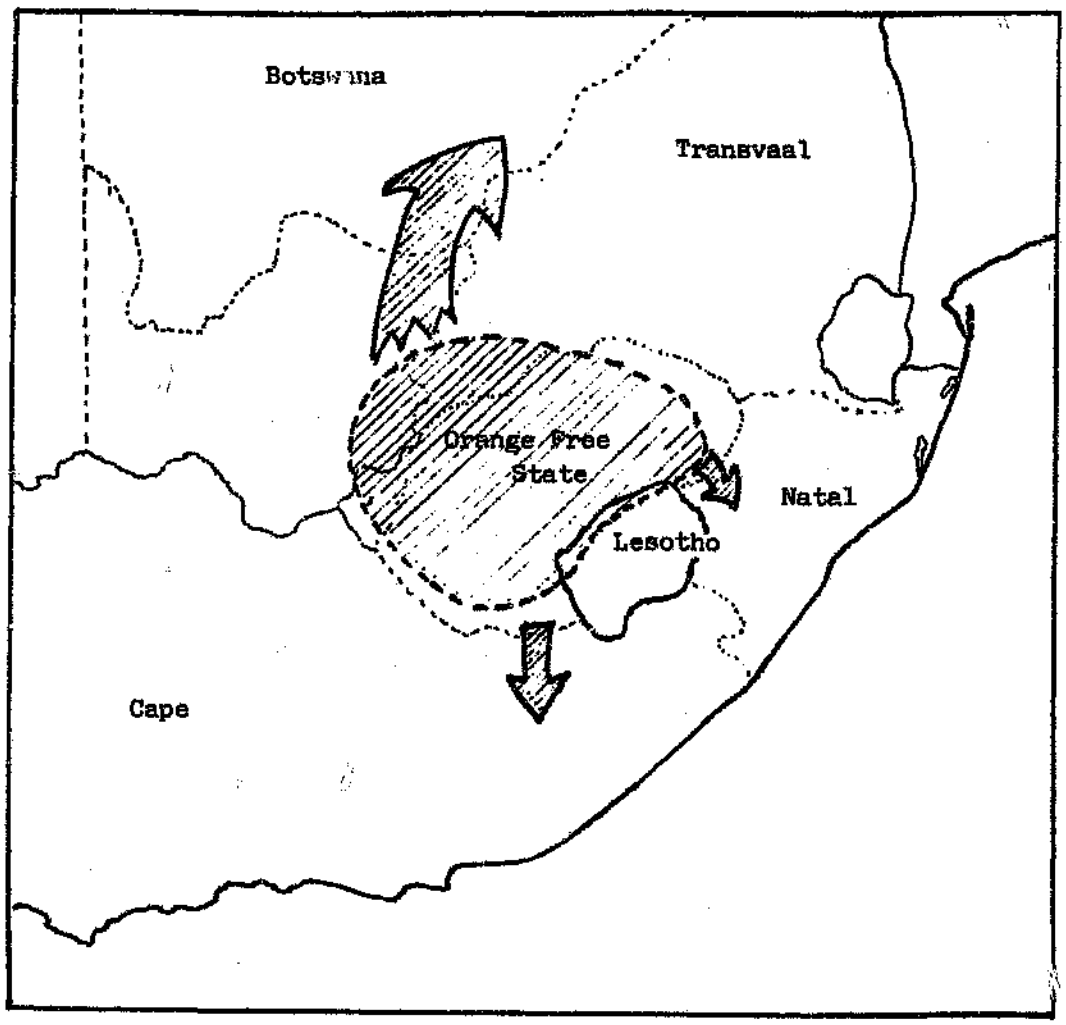

Figure 17. Probable escape routes (arrows) of peripheral populations of Bearded Woodpeckers from frost-devastated woodland (hatched area) which could have covered much of the Orange Free State in a warmer climate.

eastern Cape and northwestern Natal are derived from populations that once occupied what is now the OFS, and are not relicts of a southwestward expansion down through Natal of populations in Mozambique.

The important and significant implication of this hypothesis is that these isolated Bearded Woodpecker populations are direct descendents of the population that gave rise to the Ground Woodpecker. They have remained true to type because of their success in tracking their normal environment. The eastern Cape and Natal woodlands would have been subject to the cold climate episodes, but because of their lower altitude and relative proximity to the coast, would not have been subject to such destructive low temperature extremes as the interior plateaux.

In the meantime, those populations which did not escape from the OFS plains were forced to adapt to a treeless environment. The altered landscape was probably essentially similar to that which is to be seen there today, seemingly endless plains, relieved in places by flat-topped mesas or buttes. These geomorphological features with their rock-strewn slopes and eroded gullies, would have provided elevated perches and roosting sites, as well as shelter from prevailing cold winds on their lee sides. Some may well have supported trees on sheltered slopes when woodland on the exposed flats had already died and fallen. Because they are the only prominent features, they can be seen over considerable distances, and they would have formed the focal points of attraction for "refugee" woodpeckers, serving to bring together survivors that were probably widely dispersed over tree-denuded plains. The boulder-strewn slopes of the sandstone-capped hills would thus ultimately have formed the new environment to which the woodpeckers would adapt.

DISCUSSION

The actual manner, place and time of the origin of the Ground Woodpecker can never be known with certainty. The hypothesis advanced above is consistent with all the

evidence that can be mustered at present, and shows how and where this speciation event could have occurred. Firm evidence to support a suggestion of when the event occurred is lacking. Vrba (1985a) has stated that lineage turnover was mainly associated with two cold periods which commenced at approximately 4 Myr and 2.5 Myr ago. Brain (1985) has pointed out that at least six cold episodes of varying severity are known to have occurred in the Pleistocene in southern Africa.

Several aspects of Ground Woodpecker behaviour and distribution might imply that the species is of comparatively recent origin, but these aspects could equally well be interpreted as resulting from recent climatic oscillations. If the hypothesis is correct, however, and the isolated Bearded Woodpecker populations in the Cape and Natal are descended from contemporaries of those that gave rise to the Ground Woodpecker, then an origin in the Pleistocene, rather than the Pliocene, seems likely.

The current occurrence of common Orange Free State plateau birds in the catchment basins of the Great Fish, Kei and Tugela rivers seem to result from spill-over movements that skirt around the Lesotho highlands, and relate to the present altitudinal profile. This only came into being with the uplift of the Natal Monocline which is believed to have started at about 2.5 Myr ago, and to have coincided with global tectonic activity (Partridge 1985). The uplift amounted to 700 m and areas elevated by this amount would have been subject to a fall of 4.5°C in mean temperature by virtue of the standard lapse rate. Geomorphological evidence indicates that the uplift was gradual however; on an ecological time scale its interim affect on temperature would have been imperceptible, and although its ultimate influence on climate has been significant and lasting it is unlikely to have played a direct rôle in speciation events.

The timing of the uplift, relative to the onset of the cold episode that is estimated to have started at approximately 2.5 Myr ago, is not known. Vrba has commented

(pers. comm.) that the most recent period of lineage turnover occurred at ca. 400 000 years ago. Of the three such turnover events, this most recent one is the only definite post-uplift one and is to be prefered in terms of the aforementioned considerations. However, the Ground Woodpecker need not necessarily have evolved in concert with any of the major turnover events, though it is likely to have done so, and further speculation is unwarranted without more evidence.

o o o O o o o

9. ADAPTATION AND ITS CONSEQUENCES.

"Selection has nothing to do with what is necessary or unnecessary, or what is adequate or inadequate, for continued survival. It deals only with an immediate better-vs.-worse within a system of alternative, and therefore competing, entities. It will act to maximize the mean reproductive performance regardless of the effect on long-term population survival. It is not a mechanism that can anticipate possible extinction and take steps to avoid it."

G.C. Williams (1966). Adaptation and Natural Selection.

INTRODUCTION

The primary objective of this study has been to explore and test the idea that species originate as a consequence of adaptation of a small, isolated population to a new environment. The Ground Woodpecker has been the tool for this exploration. Aspects of its behaviour, ecology and reproductive biology have been documented in earlier chapters and an hypothesis of relationship and ancestry has been presented. It has further been suggested how and where an ancestral population could have been isolated in a treeless environment. Using the same scenario it remains now to trace the probable course of adaptation that resulted in the destabilization of the ancestral characteristics and the emergence of a bird so changed that systematists have classified it not merely as a new species but also as a new genus.

From the outset it has been made clear that the Recognition Concept of species (Paterson, 1985) is preferred to alternatives. It will not be argued that this concept is correct because the origin of the Ground Woodpecker can be explained in terms of it, but rather that

the degree to which the adaptations of this species are plausibly and logically accounted for in terms of different concepts can be contrasted to provide a valid test of these concepts.

THE ENVIRONMENT

In any situation in which an organism is restricted to an environment which differs from that to which it is adapted, it will be subject to a measure of stress. The amount of stress will be directly proportional to the degree of difference between the old and new environments. In the long term, effective adaptation to the new environment will so change the organism that features of its habitat which were initially stressful may become needed resources (Williams 1966). In the short term however, it has not only to survive but also to breed, for the persistence of an isolated population is dependant on an adequate measure of reproductive success.

Andrewartha (1984) has defined the environment as "every 'thing' that might influence the animal's chance to survive and reproduce", and has listed four kinds of 'thing' that influence the animal directly. These four major environmental components, through which all other minor and indirect factors operate, are resources, mates, predators and malentities.

For a warm-blooded vertebrate such as a woodpecker, the resources required for day-to-day survival are food and shelter. This much has already been mentioned in the scenario set out in Chapter 8. With the ultimate decay and fall of the frost-killed trees, the Bearded Woodpeckers may well have started to eat ants and are likely to have used tunnels in banks for nocturnal roosts. Breeding may have continued normally while the dead trees were still standing. After their fall however, reproductive activity probably underwent a marked reduction for two reasons: the lack of tree trunks and limbs for nest site excavation and the lack of appropriate substrate on which to drum. As aforementioned in Chapter 8, the drumming of the Bearded

Woodpecker is one of the characteristic sounds of African woodland and, as with northern temperate zone woodpeckers, it plays a role in territorial advertisement and other forms of signalling between mates. For a while, perhaps, drumming could still be performed on the harder portions of prostrate trees. Although the loss of trees would inhibit drumming, the consequent increase in visibility could promote contact between mates, especially if the birds were concentrated on the slopes of mesas and buttes, rather than widely scattered over the treeless plains.

This concentration of birds from the plains to high-rising topographical features would not have been restricted to woodpeckers. One would expect that any woodland raptors such as Goshawks, Accipiter spp., would also be drawn to these sandstone-capped hills which would already have constituted the natural haunts of falcons and buzzards. For the woodpeckers, deprived of their tree trunks (a substrate on which both their plumage pattern and agility helped them to avoid detection and attack by hawks), attacks by aerial predators would have been a significant factor of their new environment. Furthermore, by feeding largely on the ground they would also become vulnerable to terrestrial predators which previously posed little or no threat to them.

DIRECTIONAL SELECTION

Woodpeckers, as Short (1982) has pointed out, are unusually tough, hardy birds. The new environment was obviously not so harsh as to consistently preclude breeding success, but different enough to result in strong directional selection. Selection was likely to have been particularly rigorous from the outset with respect to feeding apparatus, the need for camouflage (which would primarily have involved the head plumage), and adjustment to lower temperatures. These aspects can be considered in more detail.

Feeding apparatus.

Short (1971e) considered the ancestor of the Ground

Woodpecker to have been formicivorous, and viewed the ant-eating habit as a prerequisite for a terrestrial existence. The Bearded Woodpecker, however, feeds primarily on large, wood-boring insect larvae and seldom eats ants. Most birds and mammals which have been sufficiently studied have been shown to be opportunist feeders; birds in particular, because of their superior mobility, are quick to exploit new situations. The nocturnal hawking by Hartlaub's Gulls Larus hartlaubii of flying insects attracted to street lights (Simon 1977), and nectar feeding by 73 non-nectarivorous birds including parrots, ravens and thrushes (Oatley & Skead 1972) are examples of the readiness with which birds will adopt foraging techniques for which they are not adapted in order to exploit abundant food resources. It is therefore reasonable to suppose that a bird with an extrudable tongue, used to probing the small holes and tunnels of wood-boring insect larvae, could readily switch to ant-eating if its former prey became scarce or unavailable.

The harpoon-type tongue is inefficient for the capture of small prey such as ants, but by probing ant tunnels a measure of success might have been achieved because small ants would be stuck to the tongue by the surface tension of the salivary coating. The Bearded Woodpecker does not have copious, sticky saliva and the probing of ant tunnels in soil must have taxed the capacity of its salivary glands. Without saliva the birds could not readily exploit ants; surface gleaning could only have been achieved by seizing each ant individually with the bill.

There would thus have been strong selection pressure for the enlargement and modification of existing salivary glands to enable production of glutinous saliva which would make the tongue an effective sticky trap without compromising the bird's water balance. Since large salivary glands are a characteristic of many woodpeckers, the adaptive modification of existing glands may have been facilitated by no more than the phenotypic expression of a suppressed alternative state. If this were not the case

then one may suppose that such enlarged, mucus-producing glands have arisen independently many times in the Picidae through the action of natural selection, as they have in the corvid genus Perisoreus, in which they are a unique specialization (Bock 1961).

Because terrestrial ant colonies may be sited several centimetres or more below the soil surface, there would also have been strong selection for increased tongue length. Arboreal woodpeckers adapted to feeding on wood-boring insect larvae generally have shorter tongues than similar-sized ant-eating woodpeckers. In the Bearded Woodpecker the hyoids extend over the skull as far as the midpoint of the orbits; in the Ground Woodpecker the hyoids are longer and extend past the front of the skull to insert into the right nostril.

Camouflage.

If there was severe risk of predation, as seems probable, there would have been proportionately strong selection to bring about a match between the woodpeckers' plumage and the substrate on which they were most at risk - the ground. The bright scarlet hindcrown of the male Bearded Woodpecker would have made concealment from aerial predators difficult, whilst the contrasting black and white facial markings of both sexes would have made them conspicuous at ground level.

Adjustment to low temperature.

The reduction in mean minimum temperatures which, in terms of the hypothesis advanced here, triggered the whole train of events, was presumably a persistent characteristic of the new environment and would have given rise to directional selection. Adaptation to cold might have been achieved in several ways. Wallgren (1954) has shown that energy metabolism in two european buntings Emberiza citrinella and E. hortulana, differs in keeping with their respective northern and southern distribution patterns. The significance of Wallgren's research has been seen to

lie in the demonstration that even homeotherms may have physiological adaptations to temperature regimes (Mayr 1963).

Given that such physiological adjustment to prevailing temperature of normal habitat may occur as a species-wide characteristic of a warm-blooded vertebrate, one may predict that the Ground Woodpecker differs from its ancestor, the Bearded Woodpecker, in this way. The susceptibility of the former to heat stress has been noted, and it is a bigger bird. The size difference between the two species is most apparent in mass, the Ground Woodpecker being some 40% heavier on average. Although Scholander (1955, 1956) rejected the idea that surface area/volume change and commensurate modification of heat loss is superior to other avenues of heat conservation, such as changes in circulation and tissue tolerance, larger size in the Ground Woodpecker could have been advantageous in several ways and thus been favoured by more than one type of selection pressure. For example, larger size would have contributed to a longer tongue by virtue of simple isometry and thus have conferred greater reach to the bird in its quest for subterranean ants. Increase in size could also reduce risk of predation. In terms of the scenario favoured here, these different selection pressures are likely to have been acting in concert. It is possible, however, that size increase was strongly favoured by only one type of directional selection, and its alternative advantages were merely fortuitous effects.

Because physiolgical adjustment would take time to perfect, even under strong directional selection, initial heat conservation must have been accomplished behaviourally. During the day, heat loss would have been a problem only if ambient temperature was lower than the woodpecker's zone of thermal neutrality and wind speed exceeded 4 m/sec. The birds could have sheltered from strong winds by using the lee side of rocks, as Ground Woodpeckers do. In cold but sunny conditions they could also have compensated for heat loss by squatting on sun-warmed rocks and frequenting west-facing slopes in the afternoon. Low night temperatures would have posed the greatest cold stress however.

Nothing is known about the roosting habits of Bearded Woodpeckers. During the cold, northern temperate zone winters, some Eurasian woodpeckers are known to roost alone in tree holes or artificial nest boxes and to defaecate in these sites (Matsuoka and Kojima 1979). Ground Woodpeckers roost communally and do not defaecate in their tunnel chambers. These tunnels, used for both nesting and roosting, are frequently up to one metre in length (Ch. 6), so the chamber is considerably further from outside conditions than a tree hole can be. This tunnel length insulates the chamber from the exterior temperature extremes, and the metabolic heat of the roosting birds must effectively raise the chamber temperature to within the birds' thermally neutral range. This much may be reasonably assumed from studies of chamber temperatures and gaseous environments in the tunnel nests of European Bee-eaters, Merops apiaster, by White et al. (1978).

Up to six Ground Woodpeckers have been seen to roost in one tunnel, and the same tunnel may be used every night for several months. If the birds defaecated in the chamber, two disadvantages would rapidly accrue from intensive usage of a single site: plumage soiling would become commonplace, and there would be an increase of ammonia in the chamber environment. Bee-eaters do not practice nest sanitation; White and his colleagues measured ammonia concentrations as high as 700 ppm in bee-eater nest chambers, and commented that such concentrations would be harmful to most vertebrates without special adaptations.

The potentially negative consequences of the build-up of metabolites and their breakdown products have been avoided in the Ground Woodpecker by the apparent inhibition of nocturnal defaecation. This would appear to be a species-wide characteristic and is best seen as a correlate of communal roosting in a confined space, a habit which in turn probably arose as a behavioural means of heat conservation.

CONSEQUENCES

The changes in diet, plumage pattern and colouration which resulted from confinement to a treeless environment, would have brought about the need for yet more changes. The specialization in ant-eating, for example, would have affected reproductive activities. Instead of bringing one large beetle larva to the nest (see photograph in Tarboton, 1970) with which only one of the chicks could be fed, the adult could bring a large mass of ants which, by regurgitation, could be fed in portions to each of the chicks. This method necessitates fewer visits to the nest, thus lowering the chances of its detection by predators. It also requires a fundamental change in the behaviour of the chick which, at some stage in its development, must put its beak inside that of the parent to take the regurgitated ants, instead of having a large single food item placed in its own gaping beak by the adult.

The most significant consequences, however, would result from the changes to plumage pattern and colouration, since these would affect the efficiency of signalling between mates. As aforementioned, the advertisement achieved through drumming could not be maintained in the new environment since there was no substrate on which such percussive signalling could be performed. The subsequent loss, as suggested above, of the sexually distinctive markings on the head of the Bearded Woodpecker was likely to have further disrupted the fixed signal-response system which, in normal woodland habitat, is the prerequisite for successful courtship and fertilization of the female Bearded Woodpecker by the male.

This signal-response system, the Specific-mate recognition system or SMRS (Paterson 1985), is maintained under strong stabilizing selection so long as the species stays within its normal habitat. But if the species is deprived of trees it is also deprived of its usual food, normal perching, roosting and nesting sites, concealment from predators, and sounding boards for percussive signalling.

Under such circumstances stabilizing selection on the original system is relaxed; the aggregate of new selection pressures outweighs the old and, if the population persists, some existing adapted systems will inevitably degenerate while others adjust tc the new conditions. For example, the chisel-tipped beak and related skull reinforcement which enabled the Bearded Woodpecker to find food, excavate nest sites and perform drumming would have ceased to be of any selective advantage. Likewise, the SMRS, deprived of one signal component after another, would no longer be under stabilising selection.

Directional selection is expensive. The population would remain small and probably be diminished, even given the ability of individuals to pair off and successfully raise young on a regular annual basis. A woodpecker is an animal of low fecundity, unlikely to raise more than four young in any one year. A consequence of negative directional selection, such as could result from heavy predation pressure for example, is the loss nc only of weakened or sick birds but also of many prime individuals, and the destabilization of the age structure of the population. The probability of long-term pair bonds would be reduced, especially if there was high male turnover (red-crowned males more at risk from aerial predators than black-crowned females). Surviving females might have different mates at every breeding attempt. Young birds would enter the breeding population earlier than under normal conditions. The population turnover time would be shortened and mixing would be promoted, thereby increasing the range of genetic recombination and possibly the variety of resultant phenotypes for selection to work on.

SELECTION AND GENETIC VARIANCE

Natural selection, as pointed out by Williams (1966) in the quotation that heads this chapter, is not goal-oriented. The two components of the process are the differential survival of individuals and differential reproductive success.

Under normal conditions, natural selection is acting to preserve the adaptations of the species, and any deviation from usual pattern, colouration or structure is unlikely to persist. From common experience we know that such deviations are rare. Indeed, the frequency of variants under normal conditions might seem inadequate, if maintained in a new environment, to permit directional selection to bring about change except in unimaginably long periods of time. Intuitively one would expect that if a small population experiencing negative directional selection is to adapt to its stressful environment, it must do so relatively quickly. In the case under consideration here, an upper limit can be placed on the time available, because the climatic oscillations of the Pleistocene are believed, on good evidence, to have had a periodicity of about 100 000 years (Brain 1981).

Perhaps much less time is needed. Given frequent (at least annual) and sustained genetic recombination, the rate of change would still depend on the number of phenotypic variants available for selection in the small and possibly declining population. This is the 'bottleneck' situation in which the theoretical and seemingly logical genetic consequence is going to be loss of variability. However, some recent, quantitative laboratory experiments with small founder populations of houseflies has yielded empirical evidence for an increase in variability of measured physical characteristics (Lewin 1987). It is considered that the explanation for this increase in variance may lie in non-additive gene interactions in which both dominance and epistasis could play a role. If such increase in variance proves to be a common consequence of a population bottleneck, it has exciting implications for evolutionary biology.

What could trigger such a phenomenon? Possibly it is the switch from stabilizing to directional selection. Adaptations to the old environment would degenerate to the extent that selection for their maintenance was relaxed. This might free some genetic resources which determined

the old characters and allow their participation in alternative configurations.

The possibility that dominance variance is significant in small populations under directional selection lends itself to the hypothetical course of woodpecker speciation. As mentioned in Chapter 7, some Ground Woodpeckers show traces of red colouration on the hindcrown and nape. This is best accounted for as the occasional partial expression of a masked ancestral character. Similarly, orange-red feathers can be found on the rumps of some Bearded Woodpeckers, perhaps indicating a masked character state such as is fully expressed in the sister group genus Mesopicos. In the Ground Woodpecker, the pinkish-red colouration of the rump and chest are under the same genetic control, as evidenced by the normal colouration of these parts in a partially albino bird (Ch. 7, p. 112).

SPECIATION

As a consequence of isolation in a treeless environment, stabilizing selection for certain adaptations of the Bearded Woodpecker would have been replaced by directional selection for different attributes as aforementioned. In terms of the Recognition Concept of species, the essential aspect of speciation is the change that is wrought in the communications operating between males and females. The progressive loss of components of the old SMRS has been described and was inevitable in terms of the presumed environmental conditions. The unmasking of previously suppressed characters through an increase in variance could well have supplied new patterns for natural selection to work on. Those best fitted to the new way of life and conditions of the new environment would have endured and become replacements for lost SMRS components. Calls would also have changed, with natural selection shaping the new vocalisations to the demands of the environment. Accoustic communication involves sound transmission and signal detection, and because the bird receiving the signal needs not only to detect it but also to gain information from it, there will be selection for signals that are

clearly audible at a distance against background noise such as wind (Wiley and Richards 1982). It follows also that any changes in calls will require close co-adaptation between male and female if effective communication is to be maintained.

This process would presumably have been gradual and extended over many generations. The changes from one generation to the next were probably imperceptible, for the essential requirement of recognition and response between potential mates could never have lapsed. There would always have been strong directional selection for a new SMRS for the simple reason that birds unable to find or recognise potential mates would not have contributed their genes to subsequent generations.

Ultimately, like Kipling's armadillos, the surviving woodpeckers would have been quite different from what they were before, that is to say, from what their ancestors were. They would have been relatively few in number, and had probably always been on the fringe of extinction. But as the characters under directional selection came to fulfil the demands of the new environment, so would the selection pressure shift to maintain these new characters and to eliminate deviations from them. Only when all the characters under selection for change reached the newly adapted state would this small population begin to expand, aided possibly by interludes of climatic amelioration which could facilitate dispersal to comparable habitat types elsewhere.

The normal habitat of these new woodpeckers (the only one they knew) comprised grassy hill slopes littered with boulders and blocks of rock. This geomorphological formation is widespread in southern Africa, as observed by Stark and Sclater in 1903 (heading to Ch. 2). Their comment is authoritatively corroborated by the following two extracts from a geomorphological textbook by King (1951):

"In South Africa, with its rocks of widely-differing durability and strong denudation, escarpments are common features, and plateau-and-scarp is the most typical expression of South African scenery, being found over most

of the interior and eastern marginal zone, besides wide areas elsewhere."

"The abundance of mesas and buttes in the Union is shown in the frequency with which the corresponding Afrikaans names, Tafelberg and Spitzkop occur, and attention should be directed to the numerous perfect buttes of the Cape Province and the Orange Free State, with their caps of resistant sandstone or dolerite supported upon pedestals of weak beds and their sides strewn with fallen debris."

For the new Ground Woodpeckers there was thus no lack of suitable habitat to colonise.

MODELS OF SPECIATION

The Ground Woodpecker was chosen for this study because it has obviously been involved in a dramatic evolutionary saltation. As such, it was potentially suitable for illustrating and perhaps testing Paterson's hypothesis that those properties shared by all members of a species, such as the fertilization system, and the characters that determine ecological traits and way of life, are all fixed in the speciation process, in allopatry.

The illustration has now been provided. It is hypothetical, as are all accounts of speciation. It is detailed, and may thereby incur the criticism that the evidence assembled is insufficient to justify the amount and the extent of speculative detail provided. In reply to such possible censure, it is contended that only by attempting to build a detailed and specific case upon a particular model of speciation can that model really be tested. Proponents of purely theoretical models (i.e. models based on processes for which there is no empirical support) will find such a test particularly searching. To put it another way, all models have particular sets of constraints; the degree to which a realistic scenario of speciation can be constructed within those constraints is an effective test of the model.

The prevailing orthodox genetical species concept is

loosely termed the biological species concept (Dobzhansky 1937; Mayr 1942). Paterson (1978, 1979, 1981, 1982a, 1982b, 1984, 1985, 1986) has consistently challenged the validity of this theory, which he decriptively terms the Isolation concept, and has proposed as an alternative his Recognition concept. Despite Paterson's numerous reiterations of the logical flaws of the isolation concept, many biologists seem loath to relinquish the notion that species are kept apart by isolating mechanisms. Many in fact believe that Paterson's concept is not an alternative but a restatement of the orthodox theory (Macnamara and Paterson 1984). This sort of confusion has probably arisen because of a common tendency to use the terminology of the isolation concept when evaluating the recognition concept; e.g. "The raison d'être of a mate recognition system is to prevent matings with other sympatric Drosophila." (Templeton 1979; p.516). The SMRS is not an isolating mechanism and the terms are not all interchangeable.

In the isolation concept, species are defined in terms of isolating mechanisms. As a consequence, speciation is necessarily a two-stage process. The initial stage involves divergence in at least one of two allopatric populations of a species; the divergence is not necessarily due to environmental forcing and may result, for example, from genetic drift and pleiotropy. It is supposed that the barrier (usually postulated to be geographic in nature) preventing gene flow between the two populations becomes ineffective, or is circumvented by an expansion of one or both populations so that they meet. This initiates phase 2 of the process, in which isolating mechanisms, the pleiotropic results of divergence in allopatry, are selected and reinforced to promote assortative mating. Speciation is complete when members of one population are prevented from breeding with their erstwhile brethren in the other population by a suite of isolating mechanisms, which either prevent mating or consistently reduce the success of interbreeding attempts.

In terms of this model, the evolutionary history of

the Ground Woodpecker could be very different from that just proposed. There are some difficulties, however. Let it be assumed that a small population of Bearded Woodpeckers became isolated in an area of woodland, and changed through time by the process of random mutation. How long would this take? Lande (1985) has supplied some estimates. For a population of 100 breeding individuals in a period of environmental constancy, 10^6 generations are needed for transition from one stable phenotypic state to another. If the population is doubled to 200 breeding individuals the number of generations required rises by five orders of magnitude to 10^{11}. Since there are few vertebrates with generation times of less than one year, and since the fossil record indicates vertebrate species lifespans to be of less than five to ten million years on average (Gould 1979), then either Lande's estimates are several orders of magnitude too high, or genetic drift, acting alone, plays no significant role in phenotypic divergence.

What, then, brings about divergence in allopatry? Ayala et al. (1974), in describing the two main stages of the reinforcement model of speciation, write as follows:

"First, allopatric populations of the same species become genetically differentiated, mostly as a consequence of their adaptation to different environments."

These authors demonstrated levels of genetic differentiation in keeping with the presumed levels of relationship between subspecies and species of Drosophila by counting the number of electrophoretically detectable allelic substitutions per locus that had accumulated in the course of evolution. This approach was explicitly based on the premise that species undergo continuous genetic divergence through time.

Mayr (1970), is not very explicit about the causes of divergence, but in various statements invokes adaptive shifts, ecological displacements, random mutation, selection pressures, and so on. He is much more concerned to explain how isolating mechanisms arise. For example:

"Since most genes are pleiotropic, selection pressures

against one portion of the phenotype very often affect also the genetic basis of an entirely different component of the phenotype. A genetic restructuring of an incipient species, in response to an adaptive shift, may concurrently produce new isolating mechanisms." (p. 328).

This might be taken to imply that adaptation to a new environment can bring about the divergence. But in his conclusions about speciation (p. 330) Mayr states:

"Speciation disrupts the cohesion of the gene pool by temporarily depleting its gene contents and by inevitably forcing the population into a slightly or drastically different environment."

Strict interpretation of the latter quote suggests that small isolated populations diverge because of depleted genetic content and the resulting new phenotypes are forced to seek a habitat which they can optimally exploit with their new characteristics.

Can the adaptations of the Ground Woodpecker be credibly explained in this way? Obviously not. But Mayr makes many different and conflicting statements. On page 328:

"The thesis that reproductive isolation arises as a by-product of the total genetic reconstitution of the speciating population is consistent with all the known facts."

This is one of the very few statements in which Mayr does not use the term 'isolating mechanism' although this particular statement summarises three paragraphs, all of which deal with the way isolating mechanisms arise. Mayr may well have used 'reproductive isolation' as a synonym for 'isolating mechanisms' to avoid too much repetition of the latter term. Whatever the case, it illustrates the uncritical use of terms and terminology which many subsequent writers have perpetuated, as pointed out by Vrba (1985b, p. xvi):

"While most speciationists continue to use the term isolating mechanism, the acceptance that speciation is a byproduct of population divergence, and not the product of selection for isolation, is nonetheless evident in their writings."

Because of this failure on the part of many biologists to distinguish between the functions and effects of adaptations, there are still many adherents of the model of speciation by reinforcement, the second phase of the speciation process as it is believed to occur in terms of the isolation concept.

Although this model has been challenged (Paterson 1978, 1982a, 1985; Lambert and Paterson 1984), it is appropriate here to examine the scenario of Ground Woodpecker origin and to see whether it can be plausibly explained in terms of the reinforcement model. A critical requirement of this model is the establishment of at least partial sympatry between parental and daughter populations after a measure of divergence by the latter.

One way for this to have happened would have been for an amelioration of the cold climate long enough to have allowed the re-establishment of trees in at least part of the frost-denuded area by a southward expansion of woodland from the north. This would also allow expansion of Bearded Woodpeckers into the area occupied by the daughter population. This latter population could not have expanded whilst under directional selection, though some selection pressures would have been modified with the cessation of the cold conditions.

The difficulty that arises with this re-invasion hypothesis is, of course, to postulate the degree of divergence prior to the onset of warmer climate and re-establishment of woodland. Such an event is appropriate for subspecific differentiation, but if the daughter population had progressed too far along the path to terrestrial adaptation, ecological sympatry would never have occured. If divergence in a small isolated population is assumed to be brought about by environmental forcing, resulting new character states will nearly all be habitat-related. In a case such as this, where an arboreal species is forced to adapt to a terrestrial existence, subsequent sympatry is virtually impossible since the respective normal habitats of parental and daughter populations are mutually exclusive.

Obviously it would be easier to conceive of a speciation scenario involving reinforcement (provided the probable outcome of heterozygote disadvantage is ignored) for two species with similar ecology. Indeed, all of the studies supposed to provide good supporting evidence for reinforcement involve congeneric species pairs. In consequence, it might well be contended that the major saltation involved in the origin of the Ground Woodpecker is an extreme case, and as such does not invalidate the role of reinforcement in other species' origins. However, the fallacy of such logic was pointed out (in a different context) as long ago as 1859 by J.S. Mill, one of the great philosophers of the nineteenth century, when he wrote:

"Strange it is that men should admit the validity of the argument for free discussion, but object to their being 'pushed to the extreme', not seeing that unless the reasons are good for an extreme case, they are not good for any case."

Another source of confusion evident from the writings of biologists concerns the status of subspecies. The belief that subspecies are species *in statu nascendi* has been a decoy that has misled much thought about the process of evolution. If subspecies *are* incipient species, currently in the process of becoming full species, there are some awkward implications. For example, what is driving the process of change, and will it cease when full specific status is achieved? If the answer to the latter question is in the negative, the implication is that all species must be changing all the time, as predicted by the old concept of phyletic gradualism and by the Red Queen Hypothesis (Van Valen 1973).

An alternative explanation is that subspecies *were* incipient species that did not differentiate to the extent of changing their fertilization systems, either because the habitat in which they were originally isolated differed little from that which was normal for them, or because

the isolation was of relatively short duration. It needs to be appreciated that the latter can be a result of the former; a small population under directional selection will remain small until it has adapted to its new environment. When this is accomplished it comes under stabilizing selection and can start to increase its numbers and expand its range. The process is exactly the same as for full speciation; as soon as the population begins to expand the possibility of further change (more alleles being fixed in the whole population) becomes remote. The only way a subspecies can become a full species is to re-enter the cycle of allopatric isolation involving a small population being restricted to a changed environment.

The Bearded Woodpecker - Ground Woodpecker speciation scenario set out in this and the previous chapter, provides an illustration of both full speciation by the population confined to the treeless area and probably contemporaneous subspeciation by the populations that escaped around the flanks of the Lesotho montane area to the wooded valleys of the eastern Cape and northwestern Natal (Fig. 17, p. 129).

From this it is evident that allopatric isolation and time alone do not necessarily result in speciation; there must also be a measure of habitat change. The degree of change is the critical factor; too little will result, at most, in subspeciation; too much will inevitably result in extinction. Why this is so should be obvious from a consideration of the fertilization system's close adaptedness to the environment. By contrast, there is no reason why isolating mechanisms should be expected to be related to the environment. White (1978), for example, discussing mating calls in the context of premating isolating mechanisms, states:

"In general, one would not think of an evolutionary change in the mating call of a population as being adaptive to a particular habitat."

CONCLUSIONS

The most contentious issue in evolutionary biology concerns the manner in which species originate. This study of the Ground Woodpecker, the only truly terrestrial woodpecker in Africa, has demonstrated that its derivation from an arboreal ancestor can be credibly explained in terms of adaptation by a small, allopatric population to a changed environment. Adaptations arise from natural selection working on individuals within a precise framework of habitat constraints, and are manifested as species-wide characters. These characters include:

(a) the species' coadapted fertilization system;

(b) the collective peculiarities that restrict the species to its particular, characteristic habitat, and

(c) those which determine the ecological properties of the species, or what Darwin (1859) termed the species' "place in the economy of nature."

In the Ground Woodpecker, it is apparent that the fertilization system is a combination of new and old components; the new ones involve the SMRS and include plumage characters, postures, flight displays and calls, all of which can be seen to be habitat-related; the old component involves the copulatory behaviour, and even this shows evidence of some modification related to the fact that it now takes place on rocks rather than trees (Ch. 5, p. 67).

Group (b) characters are epitomised by the Ground Woodpecker's association with rock-strewn areas and by the ways in which it uses rocks for perching, displaying, and for cover from sun, wind and avian predators. Its metabolism and general physiology, although not investigated, will probably prove to be optimum for the thermal climate characteristic of those areas where the species is most common. Its plumage colouration, roosting and nesting behaviour, are further examples of group (b) characters.

Group (c) characters are manifested primarily by the species' diet and manner of obtaining its food. The Ground

CONCLUSIONS

The most contentious issue in evolutionary biology concerns the manner in which species originate. This study of the Ground Woodpecker, the only truly terrestrial woodpecker in Africa, has demonstrated that its derivation from an arboreal ancestor can be credibly explained in terms of adaptation by a small, allopatric population to a changed environment. Adaptations arise from natural selection working on individuals within a precise framework of habitat constraints, and are manifested as species-wide characters. These characters include:

(a) the species' coadapted fertilization system;

(b) the collective peculiarities that restrict the species to its particular, characteristic habitat, and

(c) those which determine the ecological properties of the species, or what Darwin (1859) termed the species' "place in the economy of nature."

In the Ground Woodpecker, it is apparent that the fertilization system is a combination of new and old components; the new ones involve the SMRS and include plumage characters, postures, flight displays and calls, all of which can be seen to be habitat-related; the old component involves the copulatory behaviour, and even this shows evidence of some modification related to the fact that it now takes place on rocks rather than trees (C.. . , p. 67).

Group (b) characters are epitomised by the Ground Woodpecker's association with rock-strewn areas and by the ways in which it uses rocks for perching, displaying, and for cover from sun, wind and avian predators. Its metabolism and general physiology, although not investigated, will probably prove to be optimum for the thermal climate characteristic of those areas where the species is most common. Its plumage colouration, roosting and nesting behaviour, are further examples of group (b) characters.

Group (c) characters are manifested primarily by the species' diet and manner of obtaining its food. The Ground

Woodpecker's place in the environment would be described in orthodox terms as its "ecological niché". As mentioned in the first chapter, this term carries with it connotations of competition theory which, as pointed out by McIntosh (1980), has been a major stimulus in the field of theoretical ecology. Andrewartha (1984) also discusses this development but draws attention to the circular nature of the concept of competition. In the case of the Ground Woodpecker, the complexities of competition theory have no role to play. By virtue of the usually subterranean nature of its food resource and its manner of obtaining it, it has no competitors and is unique in the exploitation of this resource throughout its geographical range. There are currently no ground-foraging, ant-eating woodpeckers which are sympatric with the Ground Woodpecker, and no reasons to believe that there ever have been. The choice of diet and adaptations functioning to promote the efficient capture of ant brood are entirely explicable in terms of adjustment to a new environment.

The origin of the Ground Woodpecker is thus explained as an incidental consequence of adaptation, following the adjustment of characters of the fertilization system by directional selection to the requirements of the treeless environment in which the arboreal ancestral population had been stranded.

The recognition concept, which defines species as "that most inclusive population of individual biparental organisms which share a common fertilization system" (Paterson 1985), served as the basis for the hypothetical reconstruction of the speciation event and proved entirely adequate for the purpose. The adaptations and origin of the Ground Woodpecker are not so easily or credibly explained in terms of alternative concepts and models of speciation, however.

This study has substantially increased knowledge of the biology of the Ground Woodpecker; it has also made a contribution in the field of evolutionary biology. The demonstration that speciation can be simply accounted for

by natural selection operating at the level of the individual makes it unnecessary to invoke secondary contact with parental populations or population genetic mechanisms or other mathematically sound but biologically improbable mechanisms which theoretically might result in the origin of new species.

Finally, it is hoped that this study has illustrated how ornithology can be employed as a science of general significance to biology and not merely to those who wish to study birds. This research was motivated by the need to answer questions generated by theory and was undertaken in spite of, rather than because of the fact that very little was known about the Ground Woodpecker.

o o o O o o o

REFERENCES

ANDREWARTHA, H.G. 1984. Ecology at the cross-roads. Aust. J. Ecol. 9(1): 1-3.

ARCHER, G. & GODMAN, E.M. 1961. The Birds of British Somaliland and the Gulf of Aden. Vol. III. Oliver and Boyd. London.

AYALA, F.J., TRACEY, M.L., HEDGECOCK, D. & RICHMOND, R.C. 1974. Genetic differentiation during the speciation process in Drosophila. Evolution 28: 576-592.

BAKKER, R. 1986. The Dinosaur Heresies. Longman Scientific & Technical.

BANNERMAN, D.A. 1953. The Birds of West and Equatorial Africa. Oliver and Boyd. Edinburgh.

BENSON, C.W. & IRWIN, M.P.S. 1966. The Brachystegia Avifauna. Ostrich suppl. 6: 297-322.

BOCK, W.J. 1961. Salivary glands in the Gray Jays (Perisoreus). Auk 78: 355-365.

BRAIN, C.K. 1981. The evolution of man in Africa: was it a consequence of Cainozoic cooling? Alex L. du Toit Mem. Lecture 17. Trans. Geol. Soc. S.Afr., annex. 84, 1-19.

--------. 1985. Temperature-induced environmental changes in Africa as evolutionary stimuli In: VRBA, E.S. ed., Species and speciation, pp. 45-52. Transvaal Museum Monograph No. 4. Transvaal Museum, Pretoria.

--------. 1986. Prospects for a southern African continental record of Cainozoic temperature changes. S. Afr. J. Sci. 82: 94-96.

BROWN, C.J. & BARNES, P.R. 1984. Birds of the Natal alpine belt. Lammergeyer 33: 1-13.

BURLEY, N., KRANTZBERG, G. & RADMAN, P. 1982. Influence of colour-banding on the conspecific preferences of zebra finches. Anim. Behaviour 30: 444-455.

CAMPBELL, B. & LACK, E. (Eds.). 1985. A Dictionary of Birds. British Ornithologists' Union. T. & A.D. Poyser. Calton. 1-670.

CARSON, L.H. 1957. The species as a field for gene recombination. In: MAYR, E.; ed. The Species Problem pp. 23-38. American Association for the Advancement of Science, Publication No. 50, Washington.

CHAPIN, J.P. 1939. The Birds of the Belgian Congo. Part II. Bull. Amer. Mus. Nat. Hist. 75: 1-632.

CLANCEY, P.A. 1952. Geographical variation in the Ground Woodpecker Geocolaptes olivaceus (Gmelin), a unique South African avian endemism. Journal of the Science Society of the University of Natal 8: 3-7.

CLANCEY, P.A. 1957. Notes on some birds from the highlands of Basutoland. Ostrich 28: 135-146.

--------. 1958(a). On the status of Geocolaptes olivaceus theresae Meinertzhagen, 1949. Miscellaneous Taxonomic notes on African Birds XI., Durban Museum Novitates V: 117-118.

--------. 1958(b). The South African races of the Bearded Woodpecker Thripias namaquus (Lichtenstein). Bull. B.O.C. 78: 35-43.

--------. 1964. The Birds of Natal and Zululand. Oliver & Boyd. Edinburgh and London.

--------. 1971. A handlist of the birds of southern Mocambique. Inst. Invest. Cient. Mocamb. Lourenco Marques.

CODY, M.L. 1969. Convergent characteristics in sympatric species: a possible relation to interspecific competition and aggression. Condor 71: 222-239.

COOPE, G.R. 1979. Late Cenozoic fossil Coleoptera: evolution, biogeography, and ecology. Annual Review of Ecology and Systematics 10: 247-267.

CRACRAFT, J. 1974. Phylogenetic models and classification. Systematic Zool. 23: 71-90.

CRAMP, S. (Ed.) 1985. The Birds of the Western Palearctic. Oxford University Press. Oxford.

CROCKETT, A.B. & HANSLEY, P.L. 1977. Coition, nesting, and postfledging behaviour of Williamson's Sapsucker in Colorado. Living Bird 16: 7-19.

CYRUS, D. & ROBSON, N. 1980. Bird Atlas of Natal. University of Natal Press. Pietermaritzburg.

DARLINGTON, P.J. Jr. 1965. Biogeography of the southern end of the world. Harvard University Press. Cambridge.

DARWIN, C. 1859. The origin of species by means of natural selection. John Murray. London.

DE BRUYN, G.J., GOOSEN-DE ROO, L., HUBREGTSE-VAN DEN BERG, A.J.M. & FEIJEN, H.R. 1972. Predation of ants by woodpeckers. Ekol. Pol. 20: 83-91.

DOBZHANSKY, T. 1937. Genetics and the origin of species. Columbia University Press. New York.

DOVER, G.A. 1988. Evolving the Improbable. Tree 3: 81-84.

EARLE, R.A. 1986. Reappraisal of variation in the Ground Woodpecker Geocolaptes olivaceus (Gmelin) (AVES:PICIDAE) with notes on its moult. Navors. nas. Mus., Bloemfontein 5(7): 79-92.

EDWARDS, D. 1967. A plant ecological survey of the Tugela River basin. Botanical Survey of South Africa Memoir No. 36. Town and Regional Planning Commission. Natal.

ELDREDGE, N. & CRACRAFT, J. 1980. Phylogenetic patterns and the Evolutionary Process. Columbia University Press. New York.

ELDREDGE, N. & GOULD, S.J. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In: SCHOPF, T.J.M. ed., Models in Paleobiology pp. 82-115. Freeman. San Francisco.

EMLEN, S.J. 1972. An experimental analysis of the parameters of bird song eliciting species recognition. Behaviour 41: 130-171.

EVERY, B. 1974. A partial albino Ground Woodpecker. Ostrich 45: 192-193.

FITZSIMMONS, V.F.M. 1962. Snakes of Southern Africa. Purnell. Cape Town.

FRY, C.H. 1984. The Bee-eaters. T. & A.D. Poyser. Calton.

GAUD, J. & FAIN, A. 1989. Hyonyssus leptochaetus, n. sp. (Analgoidea, Avenzoariidae), acarien parasite des plumes du pic terrestre africain Geocolaptes olivaceus. Bull. Inst. Roy. Sci. Nat. Belgique, Entomology 58: 175-177.

GILLESPIE, J.H. 1986. Rates of molecular evolution. Ann. Review Ecol. Syst. 17: 637-665.

GLUTZ VON BLOTZHEIM, U.N. & BAUER, K.M. 1980. Handbuch der Vögel Mitteleuropas. Akademische Verlagsgesellschaft. Weisbaden.

GOODWIN, D. 1968. Notes on Woodpeckers (Picidae). Bull. Brit. Mus. (Nat. Hist.) Zool. 17(1): 1-44.

GOULD, S.J. 1979. Species are not specious. New Scientist 83: 374-376.

HAGEN, J.M. & REED, J.M. 1988. Red color bands reduce fledging success in Red-cockaded Woodpeckers. Auk 105: 498-503.

HARRIS, W.V. 1961. Termites, their recognition and control. Longmans. London.

HARRISON, R.G. 1989. Molecular Evolution. Tree 4: 6-11.

HENDEY, G.B. 1970. The age of the fossiliferous deposits at Langebaanweg, Cape Province. Ann. S. Afr. Mus. 56: 119-131.

HENNIG, W. 1966. Phylogenetic systematics. University of Illinois Press. Illinois.

HERBERT, F. 1965. Dune. Hodder & Stoughton. London.

HERHOLDT, J.J. & EARLE, R.A. 1986. Ashy Tits and Pied Barbets roosting in a sandbank. Ostrich 57: 64.

HILLIS, L.M. 1987. Molecular versus morphological approaches to systematics. Ann. Review Ecol. Syst. 18: 23-42.

IRWIN, M.P.S. 1985. Interrelationships among African species of Centropus (Cuculidae). Ostrich 56: 132-134.

JAMES, H.W. 1970. Catalogue of the birds eggs in the collections of the National Museums of Rhodesia. Trustees of the National Museums of Rhodesia. Salisbury.

JELLIS, R. 1977. Bird sounds and their meanings. British Broadcasting Corporation. London.

KEMP, M.I., KEMP, A.C. & TARBOTON, W.R. 1985. A catalogue of the birds of the Transvaal. Transvaal Museum/Transvaal Nature Conservation Division cyclostyled manuscript.

KILHAM, L. 1974. Play in Hairy, Downy and other woodpeckers. Wilson Bull. 86: 35-42.

---------. 1983. Life history studies of woodpeckers of eastern North America. Publications of the Nuttall Ornithological Club No. 20. Cambridge. Mass.

KING, L.C. 1951. South African scenery. Oliver & Boyd. London.

KINGDON, J. 1989. Island Africa. Collins. London.

KIPLING, R. 1902. Just So Stories. Macmillan. London.

LACK, P. 1985. The ecology of land-birds of Tsavo East National Park, Kenya. Scopus 9: 57-96.

LAMBERT, D.M. & PATERSON, H.E.H. 1984. On 'Bridging the gap between race and species': The isolation concept and an alternative. Proc. Linn. Soc. N.S.W. 107(4): 501-514.

LANDE, R. 1985. Expected time for random genetic drift of a population between stable phenotypic states. Proc. Natl. Acad. Sci. U.S.A. 82: 7641.

LAWRENCE, L. DE K. 1967. A comparative life-history of four species of woodpeckers. Ornith. Monogr. No. 5.

LAYARD, E.L. 1867. The Birds of South Africa. Juta. Cape Town.

LEWIN, R. 1987. The surprising genetics of bottlenecked flies. Science 235: 1325-1327.

LUSTICK, S., BATTERSBY, B. & KELTY, M. 1978. Behavioural thermoregulation: orientation toward the sun in Herring Gulls. Science 200: 81-83.

MACKWORTH-PRAED, C.W. & GRANT, C.H.B. 1952. Birds of eastern and north-eastern Africa. Vol. 1. Longmans Green. London.

MACLEAN, G.L. 1985. Roberts' Birds of Southern Africa. Trustees of the John Voelcker Bird Book Fund. Cape Town.

MACNAMARA, M. & PATERSON, H.E.H. 1984. The Recognition Concept of species. S. Afr. J. Sci. 80: 312-318.

MATSUOKA, S. & KOJIMA, K. 1979. Winter food habits of Grey-headed Green Woodpeckers Picus canus. Tori 28: 107-116.

MAYR, E. 1942. Systematics and the origin of species. Columbia University Press. New York.

--------. 1963. Animal Species and Evolution. Harvard University Press. Cambridge, Mass.

--------. 1970. Populations, Species, and Evolution. Harvard University Press. Cambridge, Mass.

MCINTOSH, R.P. 1980. Background and some current problems of theoretical ecology. Synthese 43(?): 195-255.

MEDAWAR, P.B. 1967. The Art of the Soluble. Methuen. London.

MEINERTZHAGEN, R. 1949. New races of courser, woodpecker, swift, lark, wheatear and serin from Africa. Bull. B.O.C. 69: 104-108.

MICKEY, M. R., MUNDLE, P. & ENGELMAN, L. 1981. Boolean Factor Analysis. In: DIXON, W. J. (Ed.), B.M.D.P. Statistical Software, pp. 538-546. University of California Press. Los Angeles.

MILL, J. S. 1974. On Liberty. Pelican Classics. Penguin Books. Harmondsworth.(First published 1859).

MOREAU, R.E. 1966. The Bird Faunas of Africa and its Islands. Academic Press. London.

NELSON, G. & PLATNICK, N. 1981. Systematics and Biogeography. Columbia University Press. New York.

NORTH, M.E.W. & McCHESNEY, D.S. 1964. More voices of African Birds. Laboratory of Ornithology. Cornell University.

OATLEY, T.B. 1969. Bird ecology in the evergreen forests of north-western Zambia. Puku 5: 141-180.

---------. 1970. Observations on the food and feeding habits of some African robins (Aves: Turdinae). Ann. Natal Mus. 20(2): 293-327.

OATLEY, T.B., EARLÉ, R.A. & PRINS, A.J. 1989. The diet and foraging behaviour of the Ground Woodpecker. Ostrich 60: 75-84.

OATLEY, T.B. & SKEAD, D.M. 1972. Nectar feeding by South African birds. Lammergeyer 15: 65-74.

PACKER, C. 1989. Molecular ecology. Tree 4: 156-157.

PARTRIDGE, T.C. 1985. The paleoclimatic significance of Cainozoic terrestrial stratigraphic and tectonic evidence from southern Africa: a review. S. Afr. J. Sci. 81: 245-247.

PATERSON, H.E.H. 1978. More evidence against speciation by reinforcement. S. Afr. J. Sci. 74: 369-371.

PATERSON, H.E.H. 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. S. Afr. J. Sci. 77: 113-119.

---------. 1982(a). Perspective on speciation by reinforcement. S. Afr. J. Sci. 78: 53-57.

---------. 1982(b). Darwin and the Origin of Species. S. Afr.J. Sci. 78: 272-275.

---------. 1985. The Recognition concept of Species. In: VRBA, E. S. ed., Species and speciation, pp. 21-29. Transvaal Museum Monograph No. 4. Transvaal Museum. Pretoria.

---------. 1986. Environment and species. S. Afr. J. Sci. 82: 62-65.

PETERS, J.L. 1948. Check-list of birds of the world. VI. Harvard University Press. Cambridge.

PETTERSSON, B. 1985. Extinction of an isolated population of the Middle-spotted Woodpecker Dendrocopus medius (L.) in Sweden and its relation to general theories on extinction. Biological Conservation 32: 335-353.

PRINS, A.J. 1963. A list of the ants collected in the Kruger National Park with notes on their distribution. Koedoe 6: 91-108.

RASA, A. 1985. Mongoose Watch. John Murray. London.

RICH, P.V. 1980. Preliminary report on the fossil avian remains from late tertiary sediments at Langebaanweg (Cape Province), South Africa. S. Afr. J. Sci. 76: 166-170.

SCHOLANDER, P.F. 1955. Evolution of climatic adaptation in homeotherms. Evolution 9: 15-26.

--------. 1956. Climatic rules. Evolution 10: 339-340.

SHORT, L.L. 1971(a). The affinity of African with Neotropical woodpeckers. Ostrich suppl. 8: 35-40.

--------. 1971(b). Woodpeckers without Woods. Nat. Hist. 80(3): 66-74.

--------. 1971(c). Notes on the habits of Bennett's Woodpecker in Kruger Park. Ostrich 42: 71-72.

--------. 1971(d). Notes on South African woodpeckers. Ostrich 42: 89-98.

--------. 1971(e). The Evolution of terrestrial woodpeckers. Amer. Mus. Novitates 2467: 1-23.

SHORT, L.L. 1980. Speciation in African woodpeckers. Proc. IV Pan-Afr. orn. Congr.: 1-8.

--------. 1982. Woodpeckers of the world. Delaware Museum of Natural History Monograph series No. 4. Greenville, Del.

SIBLEY, C.G. 1957. The abbreviated inner primaries of nestling woodpeckers. Auk 74: 102-103.

SIELMANN, H. 1959. My year with the Woodpeckers. Barrie & Rockcliff. London.

SIMON, D. 1977. Aerial feeding by Hartlaub's Gulls. Cormorant 3: 17.

SKAIFE, S.H. 1961. The study of ants. Longmans Green. London.

STANLEY, S.M. 1979. Macroevolution: pattern and process. Freeman. San Francisco.

STARK, A. & SCLATER, W.L. 1903. The Birds of South Africa. Porter. London.

STEINFATT, O. 1937. Aus dem leben des Grosspuntspechtes. Beit. zur Fortpfl.-Biol. d. Vögel 13: 101-113.

STEYN, P. 1982. Birds of Prey of Southern Africa. David Philip. Cape Town.

STRESEMANN, E. 1959. The status of avian systematics and its unsolved problems. Auk 76: 269-280.

SULLIVAN, K.A. 1984. The advantages of social foraging in Downy Woodpeckers. Anim. Behav. 32: 16-22.

TARBOTON, W. 1970. Notes on the Bearded Woodpecker. Bokmakierie 22: 81-84.

TYSON, P.D. [illegible]. Climatic change and variability in southern Africa. Oxford University Press. Cape Town.

TEMPLETON, A.R. 1979. Once again, why 300 species of Hawaian Drosophila? Evolution 33: 513-517.

UYS, C.J. & MACLEOD, J.G.R. 1967. The birds of the Hoop Vlei region, Bredasdorp, and the effect of the 1957 inundation over a 10-year period (1957-1966) on the distributions of species, bird numbers and breeding. Ostrich 38: 233-254.

VAN VALEN, L. 1973. A new evolutionary law. Evolutionary Theory 1: 1-30.

VRBA, E.S. 1980. Evolution, Species, and fossils: How does life evolve? S. Afr. J. Sci. 76: 61-84.

--------. 1984. Evolutionary pattern and process in the sister-group Alcelaphini - Aepycerotini (Mammalia: Bovidae) In: ELDREDGE, N. & STANLEY, S.M. (eds.) Living fossils. pp. 62-79. Springer Verlag. New York.

--------. 1985(a). African Bovidae: Evolutionary events since the Miocene. S. Afr. J. Sci. 81: 263-266.

--------. 1985(b). Introductory comments on species and speciation: In: VRBA, E. S. ed., Species and speciation, pp. ix-xviii. Transvaal Museum Monongraph No. 4. Transvaal Museum. Pretoria.

VRBA, E.S. & ELDREDGE, N. 1984. Individuals, hierachies and processes: towards a more complete evolutionary theory. Paleobiology 10(2): 146-171.

WALLGREN, H. 1954. Energy metabolism of two species of the genus Emberiza as correlated with distribution and migration. Acta Zool. Fenn. 84: 1-110.

WALTER, G.H., HULLEY, P.E. & CRAIG, A.J.F.K. 1984. Speciation, adaptation and interspecific competition. Oikos 43 (2): 246-248.

WHITE, C.M.N. 1965. A revised Check List of African non-passerine birds. Government Printer. Lusaka.

WHITE, F.N., BARTHOLOMEW, G.A. & KINNEY, J.L. 1978. Physiological and ecological correlates of tunnel nesting in

the European Bee-eater, Merops apiaster. Physiological Zool. 51: 140-154.

WHITE, M.J.D. 1978. Modes of speciation. W.H. Freeman. San Francisco.

WIENS, J.A. 1977. On competition and variable environments. Am. Scientist 65: 590-597.

WILEY, R.H. & RICHARDS, D.G. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: KROODSMA, D. E. & MILLER, H. E. (Eds.) Acoustic communication in Birds Vol. I. Academic Press. New York.

WILLIAMS, G.C. 1966. Adaptation and Natural Selection. Princeton University Press. Princeton.

WINTERBOTTOM, J.M.W. (ed.) 1969. Check List of the birds of South Africa. South African Ornithological Society List Committee.

o o o O o o o

Author: Oatley Terence Barry.

Name of thesis: The biology and relationships of the ground woodpecker.

PUBLISHER:

University of the Witwatersrand, Johannesburg
©2015

LEGALNOTICES:

Copyright Notice: All materials on the University of the Witwatersrand, Johannesburg Library website are protected by South African copyright law and may not be distributed, transmitted, displayed or otherwise published in any format, without the prior written permission of the copyright owner.

Disclaimer and Terms of Use: Provided that you maintain all copyright and other notices contained therein, you may download material (one machine readable copy and one print copy per page)for your personal and/or educational non-commercial use only.

The University of the Witwatersrand, Johannesburg, is not responsible for any errors or omissions and excludes any and all liability for any errors in or omissions from the information on the Library website.