ECOLOGY OF THE BALD IBIS *GERONTICUS CALVUS* AND FIRE IN THE SOUTH AFRICAN GRASSLAND BIOME

by

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DECLARATION

I hereby certify that this thesis is the result of my own original investigation, except where acknowledged herein, and has not been submitted for a degree from any other university.

Signed by candidate

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D. E. MANRY

ABSTRACT

The thesis comprises four separate chapters dealing with various aspects of the ecology of the bald ibis *Geronticus calvus* (Aves: Threskiornithinae) and fire in the South African grassland biome. The use of habitat by foraging bald ibises, and the reproductive performance of bald ibises during three consecutive breeding seasons (1978-80) at a single breeding colony in western Natal, South Africa, are discussed in relation to rainfall, grass-burning, domestic livestock grazing and agriculture.

A review follows dealing with the ecology of fire in the South African grassland biome, with particular reference to the possible role of lightning in the origin, maintenance and distribution of open grassland in South Africa under the natural fire regime.

The four chapters composing the thesis are prefaced by a general introduction and followed by a general summary and conclusion.

GENERAL INTRODUCTION

Ibises (Aves: Threskiornithinae) are a cosmopolitan group of birds comprising 23 extant species distributed mainly in tropical and sub-tropical regions (Mayr & Cottrell 1979).

Ibises are medium-sized birds with elongate, decurved bills, and are typically described as long-legged wading birds which inhabit wetland areas and forage in shallow water or along shorelines, consuming small fish, amphibians and invertebrates (e.g. McLachlan & Liversidge 1978). However, many species are relatively short-legged and forage primarily or exclusively on land (Archibald, Lantis, Lantis & Munetchika 1980). Most ibis species are highly gregarious, foraging in flocks, congregating in communal roosts and breeding in colonies, although at least six species are known to nest solitarily (Archibald *et al.* 1980).

The Old World genus *Geronticus* comprises two extant species with widely separated geographical distributions, but with very similar habits and morphology (Géroudet 1965, Siegfried 1971). The waldrapp or red-cheeked ibis *G. eremita* was formerly distributed widely in continental Europe, North Africa and the Middle East, but presently breeds only at one locality in Turkey, and several localities in Morocco (Géroudet 1965, Hirsch 1976, 1979, 1980, Hirsch & Schenker 1977, Schenker 1977. Smith 1970). The wintering quarters of the Turkish breeding population are supposedly in north-east Africa and the western Arabian peninsula, and are separated from the breeding area by a distance of *ca* 2600 km (Géroudet 1965, Smith 1970, Hirsch 1979, *in litt.* 1981). By contrast, Moroccan waldrapps may disperse for relatively short distances from their nesting sites during the non-breeding season, so that their breeding and wintering ranges overlap considerably (Cramp & Simmons 1977, Hirsch 1979). Waldrapps forage in arid and semi-arid sandy and gravelly plains, dry river beds, and marshy estuarine habitats and mountain plateau areas where the vegetation is sparse and short (<0,2 m), and feed mainly on insects and other invertebrates, but occasionally consume frogs, lizards, mice and other small vertebrates (Smith 1970, Cramp & Simmons 1977, Hirsch 1979, *in litt.* 1981, Hirsch & Schenker 1977).

The waldrapp's sole congenor, the bald ibis *G. calvus*, is confined to the south-eastern highlands of southern Africa (Siegfried 1971). The bald ibis does not perform long-distance, annual migrations between breeding and non-breeding areas, but undertakes short-distance, perhaps altitudinal movements within its restricted distributional range (Cooper & Edwards 1969, Siegfried 1971, McLachlan & Liversidge 1978). The feeding habits of the bald ibis are poorly known, although its diet consists primarily of insects and other invertebrates, supplemented occasionally by small vertebrates and perhaps carrion, which it locates in indigenous grassland (Layard & Sharpe 1875-1884, Stark & Sclater 1906, Vincent & Symons 1948, Cooper & Edwards 1969, McLachlan & Liversidge 1978).

Geronticus ibises usually breed in colonies ranging in size from two to 600-800 breeding pairs, although solitary nesting has been recorded in both species (Siegfried 1971, Cramp & Simmons 1977). Both species breed on vertical cliffs, and are the only ibis species that breed exclusively on cliffs (Archibald *et al.* 1980). Both species are further distinguished from more typical ibises by virtue of the fact that their breeding distributions are confined to temperate latitudes (Siegfried 1971). Finally, both species are classified as rare and threatened (King 1979), and are in urgent need of special study and conservation attention (Archibald *et al.* 1980).

This thesis documents some results of a 2½-year field study on the behaviour and ecology of the bald ibis conducted between June 1978 and December 1980 in western Natal, South Africa. The primary objectives of the study were to elucidate the foraging ecology and habitat requirements of the bald ibis by means of non-destructive observational techniques, and to gather information on the reproductive biology of *G. calvus* at a single breeding colony during three consecutive breeding seasons (1978-80). Early in the fieldwork it was noticed that bald ibises foraged extensively in burnt grassland and in short, post-burn regrowth during the annual winter and spring prescribed burning period, and an investigation was made of the role of fire in the ecology of the South African grassland biome, in an effort to elucidate the present relationship between grass-burning and the bald ibis' ecology.

The results presented herein are organised into four separate, self-contained papers, each with its own introductory, methodological, study area description and reference sections, and styled for presentation to specific journals for publication. Although this mode of presentation inevitably necessitates repetition of information between chapters, it facilitates the more rapid dissemination of the results through the scientific literature. By the time this thesis was submitted to university officials for evaluation (20th September, 1983), chapter one had been already published (*South African Journal of Wildlife Research* 12 : 85-93).

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CHAPTER 1

HABITAT USE BY FORAGING BALD IBISES IN WESTERN NATAL

1.1 Introduction

The bald ibis *Geronticus calvus* is endemic to the south-eastern highlands of southern Africa (Siegfried 1971). It is highly gregarious, usually breeding and roosting communally on cliffs and foraging in flocks (Pocock & Uys 1967, Cooper & Edwards 1969). The bald ibis is classified as rare and threatened (Siegfried, Frost, Cooper & Kemp 1976, King 1979) and is one of six endangered ibis species in need of special study and conservation attention (Archibald, Lantis, Lantis & Munetchika 1980).

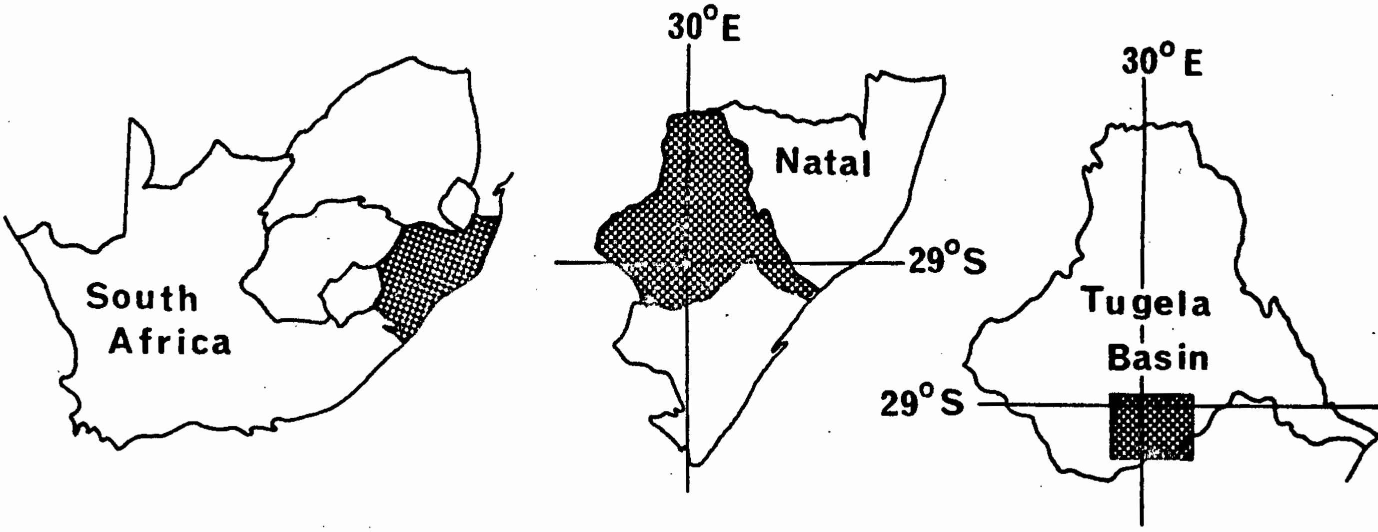
The bald ibis is primarily an insectivore, occasionally taking earthworms, snails, small vertebrates and perhaps carrion (Layard & Sharpe 1875-1884, Stark & Sclater 1906, Roberts 1940, Vincent & Symons 1948). Several observers have noted its tendency to frequent burnt grassland areas (Layard & Sharpe 1875-1884, Stark & Sclater 1906, Cooper & Edwards 1969). Here I report on the use of habitat by foraging bald ibises, and discuss relationships between fire, domestic livestock grazing, agriculture and the species' foraging ecology in western Natal.

1.2 Study area

1.2.1 Elevation, climate and vegetation

The study area straddles the watershed separating the Tugela and Mgeni River Basins in western Natal (Fig. 1.1).

Altitude ranges between 950 and 1 950 m a.s.l. Mean annual rainfall ranges between 600 and 1 000 mm, and ambient



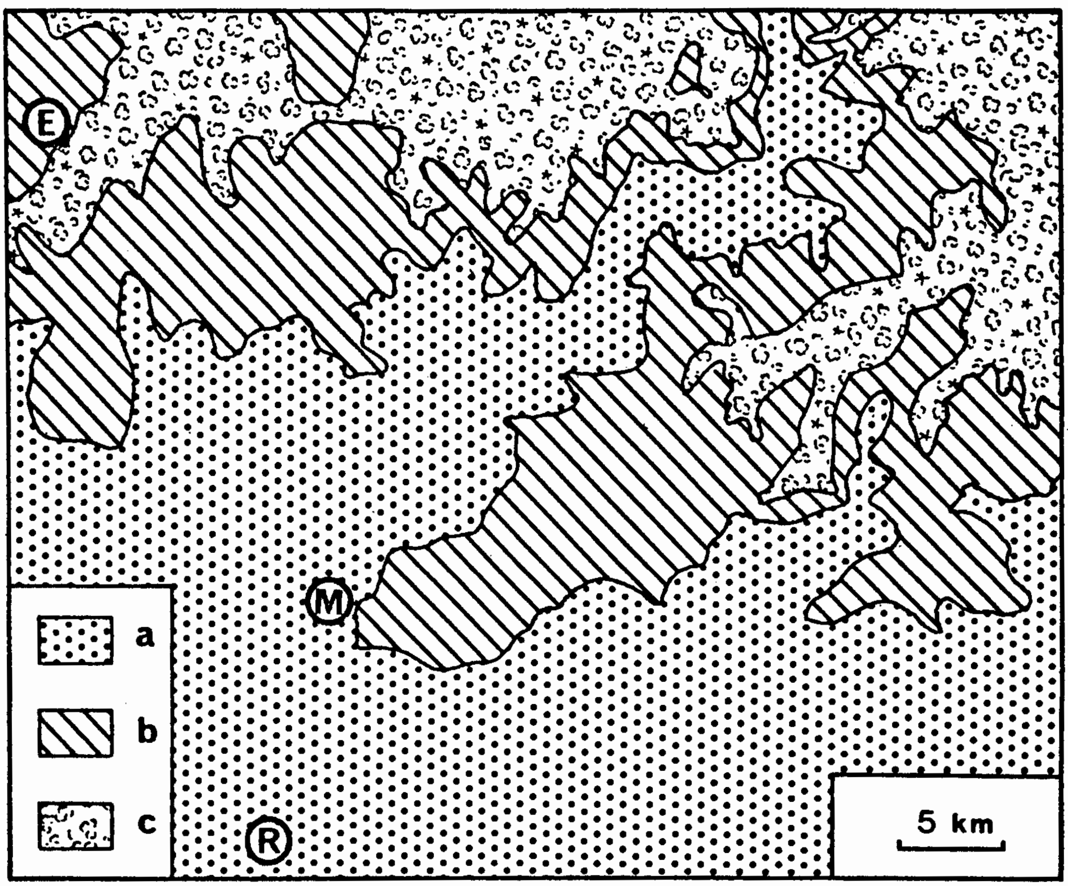


FIG. 1.1 Location of the study area and the distribution of vegetation types within the study area, after Edwards (1967) and Moll (1976). Vegetation communities are (a) *Themeda-Trachypogon* Highlands Grassland and Mistbelt Secondary *Aristida junciformis* Grassland, (b) *Themeda-Hyparrhenia* Grassland, and (c) *Acacia karroo-A. nilotica* Thorn Veld and Semi-deciduous Bush. The towns of Estcourt, Mooi River and Rosetta are indicated by 'E', 'M', and 'R', respectively.

temperature ranges from -13,3 to 45° C, with extreme local variations occasioned by altitude and topography (Edwards 1967).

The vegetation of the study area is mainly grassland (Fig. 1.1). Two basic grassland types are distinguished by Edwards (1967). *Themeda-Trachypogon* Highlands Grassland occurs between 1 400 and 1 950 m a.s.l., while *Themeda-Hyparrhenia* Grassland occurs between 1 100 and 1 500 m a.s.l. Both types are dominated by *Themeda trianda* and *Apochaete hispida*, achieving a height of 1,0-1,5 m under favourable conditions (Edwards 1967). Mistbelt *Themeda-Aristida* Grassland (Moll 1976) occurs locally in the study area in the upper Mgeni catchment (Fig. 1.1).

The remainder of the study area consists of *Acacia karroo-A. nilotica* Thorn Veld savanna and Semi-deciduous Bush (Edwards 1967) (Fig. 1.1), which occur below 1 250 m a.s.l. in the study area.

1.2.2. Fire

Grassland in the study area is a fire-maintained, sub-climax community seral to scrub-forest (in the case of *Themeda-Trachypogon* Highlands Grassland) or savanna-woodland (*Themeda-Hyparrhenia* Grassland) climax vegetation (West 1951, Killick 1963, Edwards 1967). Grassland is burnt annually by landowners, in a prescribed manner, to maintain the vigour of grasses and to discourage encroachment of undesirable plants (Tainton 1981).

Burning of vegetation in Natal is regulated by state law (Anon. 1977), and two basic types of burning are practised in the study area, viz. firebreak burning and spring burning. Firebreak burning involves the firing of strips (usually 10 - 100 m wide) for protection against runaway grassfires. Firebreaks are usually burnt from late May until mid- or late July, with the majority burnt in June, and are situated on roadsides and ridgetops, alongside marshes and streams, and around tree plantations, houses and other buildings. Preparation of firebreaks must be completed by 1 August (Anon. 1977).

Spring burning involves large expanses of grassland, to stimulate new growth for livestock. *Themeda-Trachypogon* Highlands Grassland may be burnt from 1 August to 15 October, while *Themeda-Hyparrhenia* Grassland may be burnt between 15 August and 31 October. The timing and extent of burning within the prescribed period depends greatly on the amount and distribution of rainfall (Anon. 1977). Occasional departures are made from the general prescribed burning guidelines (e.g., in 1979, "spring" burning was permitted as early as 23 July, following exceptionally heavy rainfall).

Grassland burnt in winter (late May to early August) remains dormant, with no sustained above-surface growth until mid-July or late August, when frost severity decreases and soil temperatures begin to increase (Edwards 1967). With little or no rain (as in the winter of 1980) the initial regrowth on winter-burnt grassland is meagre, while early, heavy rains (as in the winter of 1979) may stimulate lush regrowth as early as mid-July. Grassland burnt in spring (mid-August to late October) passes rapidly through the patchy regrowth stage and becomes short growth, especially if rains are copious.

The total area of grassland burnt annually is difficult to determine. In 1972, Jarman (1973) found that *ca* 29% of the total area of six highland grassland types (including *Themeda-Trachypogon* Highlands Grassland), and *ca* 12% of three "transitional" (*sensu* Edwards 1967) grassland types (including *Themeda-Hyparrhenia* Grassland) was burnt by 9 September, almost half-way into the burning season. Extrapolating the rate of grassland burning (ha burnt per day) indicated by Jarman's results to include the full duration of the burning season, *ca* 54% of the total area of highland grassland, and *ca* 36% of transitional grassland was burnt in Natal in 1972 (Table 1.1). These estimates are highly speculative, but the actual areas burnt probably fall between the amounts indicated by Jarman (1973) and the estimated values in Table 1.1.

TABLE 1.1 : Estimation of the area burnt in highland and transitional grassland in Natal during the spring burning season in 1972 (based on data in Jarman 1973).

	Type of grassland	
	Highland	Transitional
Total area (ha)	1 455 000,0	2 004 000,0
Area (ha) burnt before date of imagery	416 162,0	240 382,0
Duration (days) of spring burning season	76	78
Interval (days) between first day of spring burning season and date of imagery	40	26
Average area (ha) burnt per day	10 404,1	9 245,5
Area (ha) burnt by last day of burning season	790 707,8	721 146,0
Proportion (%) of total area burnt	54,3	36,0

The amount of grassland burnt each year can vary markedly (Edwards, in press). In 1980, very little grassland was burnt in the study area, compared with 1978 and 1979, due to the lack of rainfall.

Burning in thorn veld and Semi-Deciduous Bush is prohibited except under unusual circumstances (Anon. 1977). The occasional clandestine or accidental fire occurs in all vegetation types in the study area outside the prescribed burning periods.

1.2.3 Land-use

Cultivation is confined to a relatively small proportion of the study area, occupying approximately 14% of the total land area (Table 1.2). Approximately 74% of the study area consists of indigenous vegetation, utilised primarily for sheep, cattle and goat farming. The remainder of the study area is devoted to commercial afforestation, and non-agricultural forms of land-use (e.g. roads, settlements and reservoirs).

Maize *(Zea mays)* is the most extensive crop grown in the study area (Table 1.3). Pastures occupy approximately 6% of the study area (Table 1.2), the most important varieties being Italian ryegrass *Lolium multiflorum* (often sown in combination with oats *Avena* spp., and clover *Trifolium* spp.), Kikuyu grass *Pennisetum clandestinum*, and weeping lovegrass *Eragrostis curvula* (Table 1.3). Lucerne *Medicago sativa* is grown primarily below 1 500 m a.s.l.

TABLE 1.2 : Estimation of overall land-use in the study area (total area = 2 000 km²) (Source: Anonymous 1981).

Land-use	Area (km²)	% of total area
Indigenous vegetation	1 478,1	73,9
Crops[a]	165,2	8,3
Pastures		
Rain-fed	84,8	4,2
Irrigated	26,9	1,3
Orchards	2,0	0,1
Afforestation	123,9	6,2
Non-Agricultural	119,1	6,0

a Includes lucerne *Medicago sativa* and homogeneous oats *Avena* spp. pastures.

TABLE 1.3 : Estimated areas occupied by five different types of cultivation in the study area, and their percentage representation within the area (total area = 2 000 km²).

Type of Cultivation	Area (km²)	% of Total Area
Maize	94,38	4,72
Pastures		
Ryegrass[a]	48,59	2,43
Lovegrass	29,00	1,45
Kikuyu grass	21,14	1,06
Lucerne	3,83	0,19

a Includes ryegrass grown in combination with oats *Avena* spp. and clover *Trifolium* spp. and homogeneous oats pastures.

1.3 Methods

Between January 1979 and November 1980, I recorded all sightings of foraging bald ibises in the study area. For each sighting, I noted: date, time of day, locality, number of ibises, vegetation type, foliage height and weather conditions. Vegetation was classified as one of nine different types, based on floristic composition (Table 1.4).

For the purpose of this study, five grassland forms were distinguised on the basis of foliage height and stage of recovery after burning:

(1) Burnt grassland, with no regenerative growth is characterized by short, charred clumps of stubble (representing the bases of grass tufts) usually <30-50 mm high, interspersed with patches of bare soil and covered by a thin layer of ash.

(2) Patchy post-burn regrowth is distinguished by the appearance of new green growth in the charred grass tufts, followed by proliferation of new grass shoots.

(3) Short growth. When coverage of post-burn regrowth is approximately 80-100% (i.e. approaching uniform coverage), burnt grassland is classified as short growth. This category includes grass recovering from fire as well as unburnt grass cropped to a height of <70 mm by grazing or mowing.

(4) Medium growth occupies a height range of 70-120 mm.

(5) Tall growth occupies a height range of >120 mm.

TABLE 1.4 : Relative frequencies of bald ibises recorded in nine different vegetation types, based on totals of 168 and 134 sightings, and 2 205 and 1 859 individual birds, in 1979 and 1980, respectively.

	Percent Sightings		Percent Individuals	
	1979	1980	1979	1980
Grassland	45,8	37,3	28,57	41,26
Ryegrass Pasture	35,1	35,1	63,36	32,97
Kikuyu Pasture	4,2	6,0	0,86	1,29
Lovegrass Pasture	1,2	0,7	0,46	6,40
Sportfields & Lawns	7,7	2,2	3,76	1,18
Lucerne	-	9,0	-	14,04
Maize Fields	3,0	5,2	1,77	1,51
Ploughed Fields	3,0	1,5	1,22	0,27
Abandoned Cultivation	-	3,0	-	1,08

Cultivated habitats were classified according to the type of cultigen grown. Ryegrass pastures, ryegrass sown with clover or oats, and pure oats pastures are grouped under the heading of "ryegrass pasture". Sportsfields and lawns comprise a mixed assemblage of pastures grown for recreational and ornamental purposes. Ploughed fields were recognized by the lack of cultigen growth, while abandoned cultivation supported various stages of the secondary succession on disused fields (West 1951, Edwards 1967).

Foliage height was recorded as one of six different categories: 1 = bare substrate, little or no vegetative cover; 2 = up to the bird's heel (<70 mm); 3 = up to the bird's belly (70-120 mm); 4 = up to the bird's back (120-270 mm); 5 = up to raised head height (270-420 mm); and 6 = higher than bird's raised head (>420 mm). The approximate dimensions were derived from photographs of foraging bald ibises, assuming an average tarsus length of 70 mm (McLachlan & Liversidge 1978) and extrapolating this measure to the different height categories. Sometimes ibises occurred in unevenly grazed grassland or in pastures where short-cropped grass was interspersed with tussocks of tall, ungrazed foliage. In such cases an "average" value for foliage height was determined subjectively for the group as a whole, based on the height of the foliage where the ibises were actually feeding (short-cropped grass was preferred to ungrazed tussocks).

In some cases a group of foraging ibises would be dispersed in two different vegetation types (e.g. a maize field and adjacent grassland), or in homogeneous vegetation with distinct areas of different foliage height (e.g. a firebreak and adjacent unburnt grassland). In such cases, the total group size was sub-divided accordingly. Thus, 289 sightings yielded 302 separate records of vegetation use, and 298 records of occurrence in different foliage height categories.

TABLE 1.5 : Proportion of bald ibises recorded in each habitat type per month in 1979, expressed as percentages of total individuals recorded each month.

	MONTH											
	J	F	M	A	M	J	J	A	S	O	N	D
Grassland	100,0	67,6	78,0	2,9	0,3	49,5	45,1	74,2	84,6	33,3	24,9	9,1
Ryegrass Pasture		18,9	6,0	93,2	91,4	34,4	16,8		15,4	66,7	75,1	87,0
Kikuyu Pasture		7,8	2,0									
Lovegrass Pasture		1,3	14,0									
Sportsfields & Lawns		0,9		3,9	6,7		8,0	22,7				3,9
Maize Fields						16,1	18,6	3,1				
Ploughed Fields		3,5			1,6		11,5					
Total sightings	3	24	9	11	21	4	24	17	6	25	14	10
Total individuals	62	232	50	383	384	93	113	97	13	270	277	231

TABLE 1.6 : Proportion of bald ibises recorded in each habitat type per month in 1980, expressed as percentages of total individuals recorded each month.

	MONTH										
	J	F	M	A	M	J	J	A	S	O	N
Grassland	78,6	67,4	35,9	19,0	97,1	72,9	91,0	6,1	8,4	2,1	23,4
Ryegrass Pasture		3,4	48,3	9,7		1,2		51,5	83,3	93,7	70,3
Kikuyu Pasture	4,8	0,2	4,0	0,6				18,2			
Lovegrass Pasture		28,6									
Lucerne		0,2	11,8	63,0					2,8	4,2	6,3
Sportsfields & Lawns				6,4	2,9						
Maize Fields						14,1	9,0	24,2	1,4		
Ploughed Fields		0,2		1,3							
Abandoned Cultivation	16,6					11,8			4,1		
Total sightings	5	13	20	20	5	11	5	8	15	13	19
Total individuals	42	416	323	311	70	85	78	33	72	143	286

Most sightings were made while travelling on a motorcycle, and the remainder from either a motor-car, or while hiking on foot. Observations were aided by 8 x binoculars, sometimes supplemented with a 15-60 x zoom telescope. In addition to my own observations, 35 sightings made by reliable observers are included in the data.

1.4 Results

1.4.1 Vegetation types used by foraging bald ibises

Indigenous grassland and ryegrass pastures were the vegetation types used most frequently by foraging bald ibises (Table 1.4). Grassland was used most frequently during late summer (January-March), and during the winter and spring burning period (June-October) (Table 1.5 & 1.6). Burnt grassland was used extensively during the winter burning period in both years (Tables 1.7 and 1.8), but declined in importance after July. Patchy post-burn regrowth was used during its restricted period of availability during August-October (Tables 1.7 & 1.8), and was particularly prominent in 1979, but was of minor significance in 1980, probably as a result of the general lack of grass burning in that year.

Bald ibises foraged in short grassland throughout the year (Tables 1.7 and 1.8), although sightings were not recorded in June or August. Use of short grassland was particularly evident during September-November 1979, when the ibises fed extensively in short, uniform regrowth in areas of spring-burnt grassland. This effect was less marked and somewhat delayed in 1980, when less grassland was burnt, compared with 1979.

Outside the burning season, short growth is available in areas subjected to heavy grazing by livestock and mechanical mowing. Medium and tall grassland were of minor significance

<u>TABLE 1.7</u> : Proportion of bald ibises recorded in five different grassland sub-types in 1979, expressed as percentages of total individuals recorded per month. Monthly totals equivalent to proportion of total individuals recorded each month in grassland (See Table 1.5).

	MONTH											
	J	F	M	A	M	J	J	A	S	O	N	D
Burnt grassland						49,5	37,1	6,2	23,1			
Patchy post-burn regrowth								67,0	46,1	0,7		
Short growth		3,5	8,0		0,3				15,4	32,6	22,0	0,4
Medium growth	48,4	29,3	64,0	2,9			8,0	1,0			2,9	8,7
Tall growth	51,6	34,8	6,0									
Total	100,0	67,6	78,0	2,9	0,3	49,5	45,1	74,2	84,6	33,3	24,9	9,1

TABLE 1.8: Proportion of bald ibises recorded in five different grassland sub-types in 1980, expressed as percentages of total individuals recorded per month. Monthly totals equivalent to proportion of total individuals recorded each month in grassland (See Table 1.6).

	MONTH										
	J	F	M	A	M	J	J	A	S	O	N
Burnt grassland						49,4	66,7		2,8	1,4	
Patchy post-burn regrowth								6,1	2,8		
Short growth	28,6	67,4		0,6			24,3		2,8	0,7	23,4
Medium growth	50,0		34,0	9,7	61,4						
Tall growth			1,9	8,7	35,7	23,5					
Total	78,6	67,4	35,9	19,0	97,1	72,9	91,0	6,1	8,4	2,1	23,4

during the winter and spring burning period (Tables 1.7 & 1.8), but medium growth was an important habitat type during January-May in both years. Tall growth was used only during January-June.

Ryegrass pastures were available and used throughout the year by bald ibises (Tables 1.5 & 1.6). The annual pattern of occurrence in ryegrass pastures was bimodal, with peak use in autumn and late spring-early summer. Kikuyu grass pastures were used during January-April (Tables 1.5 & 1.6) and apparently were ignored during late spring and early summer. A similar arrangement applied in the case of lovegrass pastures (Tables 1.5 and 1.6).

Sportsfields and lawns were available throughout the year, but most sightings in this habitat type were made during April - August (Tables 1.5 & 1.6). Lucerne was grown extensively in the study area in both years, but records of bald ibises in lucerne were confined to 1980 (Table 1.6). Seasonal variation in the use of lucerne was similar to that observed in ryegrass pastures in the same year.

Bald ibises were never seen feeding in amongst growing maize plants, but foraged in reaped maize fields during the winter harvesting season. Typically, the cut stalks stand 0,2 - 1,5 m above the ground-surface, and are arranged in parallel rows *ca* 1 m apart. The soil surface is littered with dried stalks, leaves and other debris, and is devoid of most live growth during winter.

Ploughing occurred throughout the year, although most lands were ploughed during August-November for spring planting of crops. However, ploughed lands were used infrequently only during February-July (Tables 1.5 & 1.6), and apparently were avoided during the main ploughing season. Four sightings (involving a total of 20 individuals) recorded in abandoned cultivation during 1980 (Table 1.6) revealed no obvious seasonality in the use of this habitat type.

1.4.2 Foliage height

Bald ibises foraged most often in areas where the vegetation was short or virtually nonexistent (Fig. 1.2). Records in height category 1 (bare soil with little or no vegetation growth) were confined to ploughed lands and reaped maize fields. The remaining foliage height categories represent different stages of growth in grassland, pastures and abandoned cultivation.

The extent to which bald ibises occurred in the different foliage height categories varied seasonally (Fig. 1.3), and was related closely to seasonal variation in the types of vegetation used. Selection for categories 1 and 2 was most marked during June-November, primarily as a result of foraging in burnt grassland, post-burn regrowth and reaped maize fields. During the remainder of the year, categories 3 and 4 were the most frequented, when ibises fed extensively in moderately grazed grassland and pastures. The tallest height categories, 5 and 6, were frequented only during November-April, after the annual burning season, when burnt grassland and short, post-burn regrowth are unavailable.

1.5 Discussion

1.5.1 Attributes of habitats used by foraging bald ibises

Most ibis species forage in shallow water and along shorelines, consuming small aquatic animals (Archibald *et al.* 1980). My results indicate that *G. calvus* is a dry land forager, and resorts to water only for drinking and bathing.

A consistent feature of the numberous sites where bald ibises were recorded feeding was the short height of the vegetation. Bald ibises preferred vegetation shorter than the height of their abdomens, and seldom ventured into

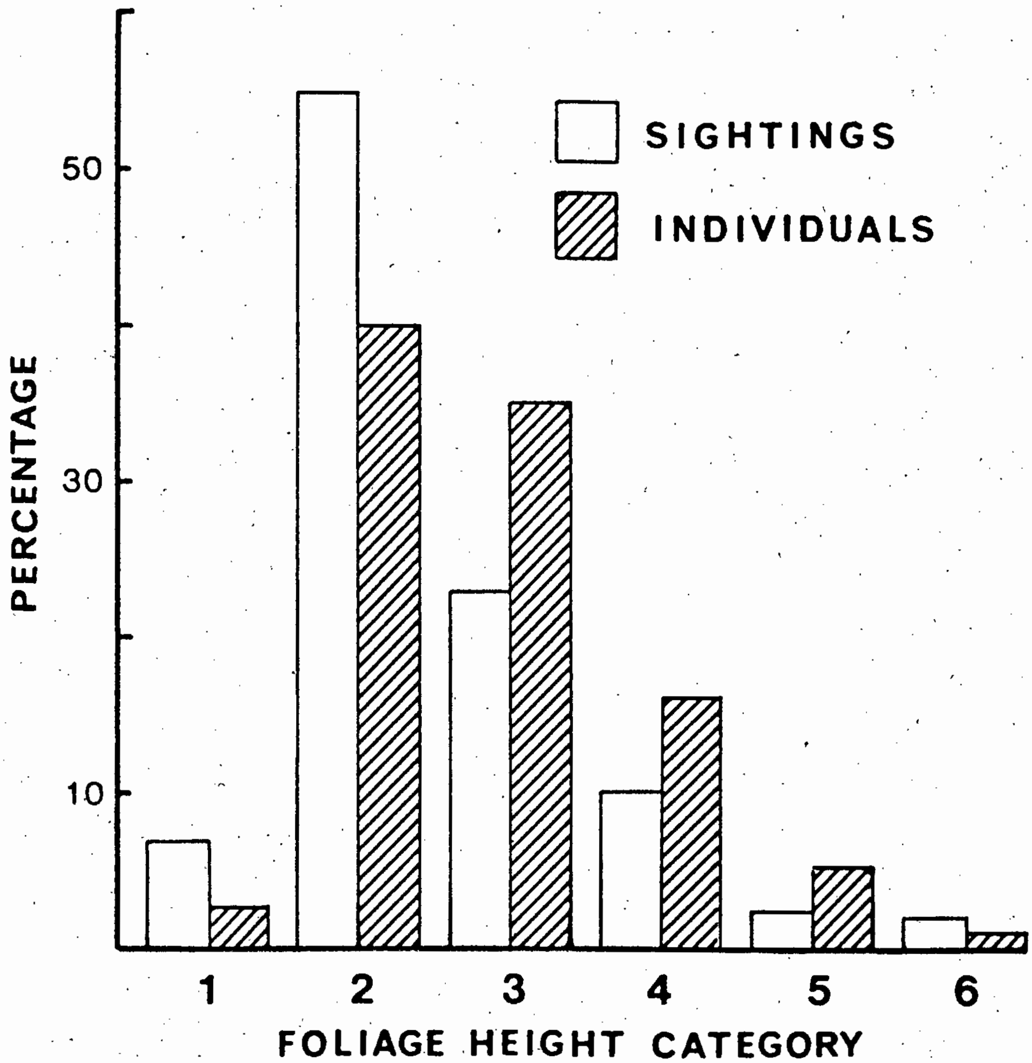


FIG. 1.2 Relative frequency of bald ibises recorded in each foliage height category, based on 298 sightings and 4 064 individuals observed during 1979-80.

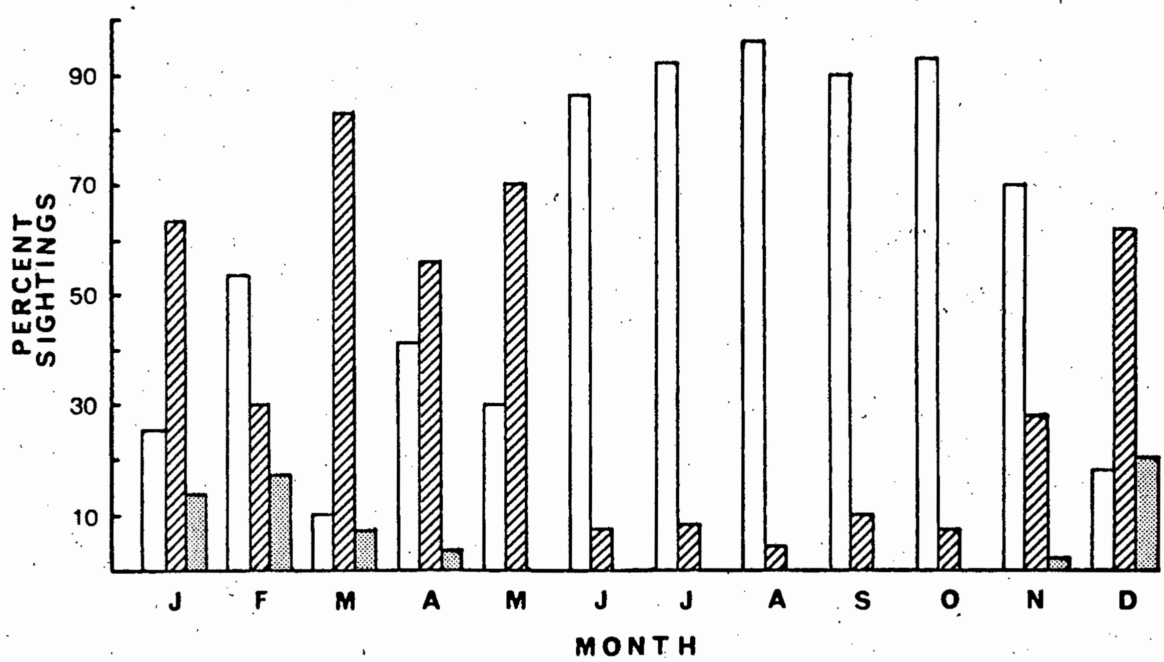


FIG. 1.3 Relative frequency of bald ibises recorded each month in foliage height categories (i) & (ii) (clear columns), (iii) & (iv) (hatched columns) and (v) & (vi) (stippled columns) during 1979-80.

vegetation higher than their backs. Given areas with equal prey densities, bald ibises presumably feed more efficiently in "short" vegetation than in "medium" or "tall" growth. Tall, dense vegetation impedes the mobility of the predator (Cody 1968), and provides concealment for prey. Unless prey is super-abundant, tall vegetation may require that the predator adopts a slow-walk-and-careful-search strategy to realize economical prey capture rates. However, in short vegetation, or on a bare substrate, the stepping rate increases, increasing the area-sampling rate, and searching time decreases. Furthermore, in short vegetation, bald ibises may be less vulnerable to predation than in tall vegetation.

Another consistent feature of the sites frequented by foraging bald ibises was the relative lack of trees. Vincent & Symons (1948) and Cooper & Edwards (1969) also mention the species' preference for open, treeless terrain. Tall trees of *Acacia sieberana* are scattered throughout *Themeda-Hyparrhenia* Grassland, particularly in the dry faciation, but they are spaced widely and almost never form an interlocking canopy. In *Themeda-Trachypogon* Highlands Grassland, trees are normally confined in their natural state to isolated patches of scrub-forest on steep slopes. Since European settlement in the mid-19th century, several varieties of non-indigenous trees have been planted extensively in both grassland types. Thus, in many places, these grassland areas are now well covered in trees. Furthermore, large areas of *Themeda-Hyparrhenia* Grassland have been invaded secondarily by thorn veld (Edwards 1967). The reduction of grassland areas through bush or karroid encroachment (Siegfried 1971), and commercial afforestation, reduces the area of suitable foraging habitat for bald ibises, and may contribute to the decline of local populations.

1.5.2 Seasonal use of pastures in relation to primary production

Of the cultivated habitat types used by bald ibises, ryegrass pastures were used most frequently. The birds' heavy reliance on ryegrass pastures during autumn (March-May) and spring (September-November) is remarkable, considering that this habitat type occupies less than 2,5% of the study area. The bimodal pattern of the use of ryegrass pastures reflects the annual pattern of net aerial production in ryegrass, which peaks during spring and autumn, with minimal growth obtaining during summer and autumn (Tainton, Bransby & Booysen 1976, Jones, Arnott & Klug 1980). Kikuyu grass differs from ryegrass in that net aerial production achieves its annual peak during late spring and summer (November-February), declines in autumn and is suspended during winter (Tainton *et al.* 1976, Jones *et al.* 1980). Kikuyu grass pastures were used during January-April, following the summer peak in production, and were apparently ignored during late spring and early summer, when productivity increases after winter dormancy. A similar arrangement applied in the case of lovegrass pastures, in which seasonal growth is similar to that obtained in Kikuyu grass (Tainton *et al.* 1976, Jones *et al.* 1980).

Verbeek (1973) documented a close correlation between the seasonal abundance of invertebrates and primary production in Californian grassland. Thus, the relationship between primary production in pastures and their use by bald ibises could be mediated by fluctuating prey abundance resulting from seasonal variation in net aerial production, although additional factors, such as grazing and mowing intensity, and the availability of alternative habitat types, are also involved. In this connection, it may be significant that Kikuyu grass and lovegrass pastures were used most extensively during January-February, when productivity and use of ryegrass pastures were low.

1.5.3 Fire in the provision of foraging habitat

Bald ibises foraged preferentially in burnt grassland and in post-burn regrowth when these habitats were available, presumably because they are more "profitable" than alternative types. The profitability of habitat for a forager is expressed as the amount of food (in biomass, calorific or nutritional units) that can be gathered per unit time spent searching in that habitat (Royama 1970). Presumably, enhanced profitability of burnt grassland and post-burn regrowth for bald ibises could be related to fire-induced structural changes in the vegetation, as well as the immediate and short-term effects of fire on prey communities inhabiting grassland. The passage of fire converts tall, dense grass into short, sparse stubble, reducing cover for invertebrates and improving conditions for the ibises' mobility.

The immediate and short-term effects of grassfires on invertebrates inhabiting African grasslands are virtually unstudied (Frost, in press). However, studies in temperate North American grasslands (Rice 1932, Tester & Marshall 1961, Cancelado & Yonke 1970) indicate that following an initial decline immediately after burning, macro-invertebrates subsequently increase, and become abundant once spring regrowth sets in. Furthermore, many invertebrates are killed by the fire, and these are readily consumed by bald ibises. Thus, the availability of prey in burnt grassland and in post-burnt regrowth is sufficient to repay attention from foraging bald ibises, and the density of prey may actually exceed that obtained in adjacent, unburnt areas.

The possible factors accounting for a greater abundance of macro-invertebrates in post-burn regrowth, compared with unburnt grassland, are worth considering here. Spring regrowth generally appears earlier in burnt areas than in unburnt areas (Rice 1932, Cook 1939, West 1965, Daubenmire

1968), providing favourable conditions for phytophagous insects relatively early in the season. Earlier resumption of leaf growth (and hence food for phytophagous insects) may result in a relatively early build-up of invertebrate numbers in burnt areas, compared with unburnt areas. Indeed, Rice (1932) noted the early appearance of several taxa (Tipulidae, Hemiptera, Homoptera and Orthoptera) in post-burn regrowth, compared with unburnt grassland.

A second factor that may influence the early occurrence and greater abundance of macro-invertebrates in post-burn regrowth, compared with unburnt areas, is the relatively high nutritional value of renewed spring growth after burning (West 1965, Daubenmire 1968, Mentis 1978). In this connection, three species of antelopes inhabiting fire-maintained grassland in highland Natal exhibit a highly significant preference for new growth in winter- and spring-burnt grassland (Oliver, Short & Hanks 1978), and Mentis (1978) showed that the crude protein and phosphate levels are higher in post-burn regrowth than in the new growth of unburnt herbage. Furthermore, preference for winter- and spring-burnt grassland by antelopes persists to the following autumn (Oliver *et al.* 1978). Similarly, winter and spring burning could affect the distribution and abundance of invertebrates (and selection of foraging sites by bald ibises) for several months after the burning season.

In addition, microclimate, and particularly the temperature regime, may favour the occurrence and productivity of invertebrates in burnt grassland, especially in winter. Ground-surface temperatures are substantially higher during the day (Phillips 1930, Mentis & Bigalke 1979) and increase more rapidly in the morning (M.J. Savage 1981, pers. comm.) in burnt than in unburnt areas, and could favour insects and other small ectotherms during the cold winter months in the study area. Ground-surface temperatures may range lower at night in burnt than in unburnt areas (Phillips 1930), but this may not be critical for organisms which are inactive at night. Also, at night, insects shelter under ash and other debris, or around the bases of grass tufts, and so probably ameliorate the effects of low temperatures.

1.5.4 Modern and pre-modern foraging ecology of *G. calvus*

The results show that bald ibises forage primarily in habitats modified by man through fire, grazing and agriculture. Because the incidence and seasonality of these three factors, and particularly fire, exert a strong influence on the timing of reproduction and migration in *G. calvus*, their pre-modern aspects are worthy of discussion.

The grasslands of Natal are burnt regularly by land managers to promote new growth for livestock, and to prevent encroachment of undesirable plants. However, there is considerable evidence to suggest that these sub-climax grasslands owe their existence to the recurrent incidence of fire (Phillips 1930, West 1951, Tainton & Mentis in press), and that lightning played an important role in the formation of fire-maintained grassland in South Africa (Bayer 1955, Killick 1963, West 1965, Mentis, Meiklejohn & Scotcher 1974). Thus, it seems likely that fire has been a regular feature of the bald ibis' grassland biotope for considerable time, and that the present, artificial fire regime is modified from a pre-existing, "natural" fire regime (West 1965, Mentis *et al.* 1974).

Domesticated caprines (sheep or goat) and cattle were present 1 200 - 1 400 years B.P. in Natal, and may have been introduced as early as 1 700 - 1 800 years B.P. (Maggs 1980). Prior to the introduction of domesticated livestock, the grasslands of the study area, and the rest of South Africa, were inhabited by a diverse and abundant community of grazing ungulates which were largely migratory (Du Plessis 1969).

Thus, grazing by large ungulates, and the subsequent short-grass conditions have been features of the bald ibis' environment for a long time. It is interesting that the black wildebeest *Connochaetes gnou* shows a marked preference for short, heavily grazed grassland created and maintained by the wildebeests themselves (von Richter 1971). Since the former range of the black wildebeest (Du Plessis 1969) coincides to a large extent with the distribution of *G. calvus* (Siegfried 1971), it is possible that *G. calvus* may have been associated closely with the short-grass areas created by wildebeests. Furthermore, the daily movements of most grazing ungulates are restricted by the availability of surface water, especially during the dry season (Western 1975), so that short-grazed grass is normally available around pans and vleis. Such heavily grazed areas may be profitable foraging habitats for bald ibises. Several studies (cited in Tester & Marshall 1961) indicate that grasshoppers are more numerous in heavily grazed than in undisturbed grassland.

Compared with fire and grazing, agriculture is a relatively recent development in the study area. Iron age farming communities arrived in Natal *ca* 1 600 - 1 700 years B.P. (Maggs 1980). These earliest farmers probably cultivated grains, legumes, and cucurbits, and confined their settlements to the Semi-deciduous Bush until *ca* 1 000 years B.P. After that date, iron age settlements expanded into the Interior *Acacia karroo*-*A. nilotica* Thorn Veld, and *Themeda*-*Hyparrhenia* Grassland, up to the present boundary of *Themeda*-*Trachypogon* Highlands Grassland (Maggs 1980). It is reasonable to speculate that the bald ibis' postulated older association with discrete, patchily distributed foraging habitats, created by fire and localized grazing, predisposed the species to feeding regularly in cultivated lands.

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CHAPTER 2

FACTORS INFLUENCING THE USE OF WINTER-BURNT GRASSLAND BY BALD IBISES

2.1 Introduction

The bald ibis *Geronticus calvus* (Aves: Threskiornithidae) is a rare species endemic to the southeastern highlands of southern Africa. It is highly gregarious, usually feeding in flocks and roosting communally on cliffs and in trees. The bald ibis inhabits open grassland areas, and feeds primarily on arthropods, earthworms and other small invertebrates obtained in grassland and cultivated lands (Vincent & Symons 1948, Siegfried 1971, McLachlan & Liversidge 1978, Manry 1982).

The grassland inhabited by *G. calvus* is burnt annually by landowners, usually between May and November, and the bald ibis feeds extensively in burnt grassland and in short, post-burn regrowth during the prescribed burning period (Manry 1982). This paper investigates the use of winter-burnt grassland by foraging bald ibises, and changes in arthropod abundance in winter-burnt grassland, in relation to the time elapsed after burning.

2.2 Study area and grass-burning

The study area is in western Natal, South Africa (Manry 1982). Altitude ranges between 950 and 1 950 m above sea level, and ambient temperature ranges from - 13,3 to 45,0°C. Mean annual rainfall ranges between 600 and 1 000 mm; approximately 48% of the total annual rainfall occurs in summer (December-February), whereas 5-6% occurs during winter (June-August). Frosts are severe during winter, but snowfalls are extremely rare in the study area (Edwards 1967; Manry 1982).

Approximately 74% of the study area consists of indigenous grassland and savanna-woodland vegetation (Manry 1982). In its natural condition grassland is virtually devoid of trees, but plantations of conifers, eucalypts and other non-indigenous trees are now commonplace in grassland since the arrival of European settlers in the mid-19th century (Edwards 1967). Approximately 26% of the study area is under cultivation, silviculture and non-agricultural forms of land-use (Manry 1982).

During autumn (March-May) grass in the study area becomes desiccated and highly flammable. Landowners burn strips of grassland (usually between 10 and 100 m wide) during May-July to create a network of firebreaks for protection against runaway grassfires. Firebreaks burnt during June-July, and large areas of grassland burnt inadvertently when firebreaks are prepared, are herein referred to collectively as "winter-burnt grassland". Grassland burnt during this period remains dormant, with no sustained aerial regrowth, until rain and/or rising soil temperature stimulate the resumption of aerial growth sometime between mid-July and mid-August (Edwards 1967, Manry 1982).

2.3 Methods

From June 1978 to November 1980 I recorded all sightings of bald ibises foraging in the study area. For each sighting I noted the date, time of day, locality, the number of ibises present and habitat type (Manry 1982). Where ibises were observed feeding in dormant burnt grassland an attempt was made to contact the property owner to ascertain the date of burning.

Invertebrates were sampled on four different firebreaks burnt between 2 June and 6 July 1980 on the farm "Durleigh" (29° 15' S, 29° 55' E; 1 450 m above sea level) in *Themeda-Trachypogon* Highlands Grassland (Edwards 1967), approximately

10 km SW of Mooi River, Natal. *Themeda-Trachypogon* Highlands Grassland is dominated by *Themeda trianda*, *Apochaete hispida*, *Trachypogon spicatus* and *Heteropogon contortus*, and achieves a height of 1,0 m under favourable conditions (Edwards 1967). Samples were collected systematically during June-August 1980 using a bottomless cardboard carton (580 x 380 x 380 mm wide) with a removable top. The sampling box was suspended on the end of a 2 m pole, carried along the midline of the firebreak and dropped to the ground suddenly at *ca* 10 m intervals. The top was then removed and any living or dead macrofauna with a combined head-abdomen length of ≧ 5,0 mm were collected and posited in glass vials (the minimum size criterion eliminated micro-invertebrates such as collembolans and formicids from the samples). Ash and other detritus were dislodged and removed by gentle blowing and sweeping with a small paintbrush, and any dead invertebrates, as well as living invertebrates sheltering around the bases of grass tufts, were collected.

Thirty samples were collected from each firebreak in each sampling trial. No attempt was made to investigate possible diurnal variation in the abundance of live invertebrates on firebreaks, although samples from a given sampling trial on a particular firebreak were collected at different times of the day (e.g. 15 in early morning, 15 at mid-day) to help ameliorate the effects of possible diurnal movements of invertebrates between firebreaks and the surrounding unburnt grassland.

2.4 Results

2.4.1 Use of winter-burnt grassland by foraging bald ibises

Bald ibises feeding in dormant burnt grassland during winter were encountered singly or in groups ranging in size from two to 52 individuals (mean ± S.D. : 9,17 ± 12,12 ; n = 30).

Of a total of 30 sightings of bald ibises feeding in dormant burnt grassland during June-August in 1978, 1979 and 1980, the age of the burn was determined in 23 separate cases, involving a total of 180 individuals (Fig. 2.1). The majority of these sightings (52%) and individuals (73%) were recorded within one week of burning, while six sightings (involving a total of 43 individuals) were recorded in dormant burnt grassland 2-24 hours after burning. The remaining records were made between one and 35 days after burning (Fig. 2.1).

2.4.2 Arthropods in winter-burnt grassland

A total of 360 samples was collected in 12 sampling trials on four different firebreaks. All macrofauna collected were arthropods, with acridids, blattids, lepidopterous larvae and spiders being the most numerous (Table 2.1). Acridids, blattids, curculionids and spiders were recorded in 33-75% of all sampling trials (Table 2.1).

Samples were assigned to three different groups, viz. those collected 0-7 days after burning, those collected >7 days after burning but prior to the resumption of sustained aerial growth (i.e. 14-37 days after burning), and those collected in the early stages of renewed aerial growth (46-82 days after burning) (Table 2.2). These data indicate some possible trends in the availability of potential food items for bald ibises in winter-burnt grassland. Of particular interest is the relatively high abundance of dead invertebrates in winter-burnt grassland during the first week after burning, which declines rapidly during the following weeks (Table 2.2). Similarly, live invertebrates were most numerous during the initial week after burning, but were substantially less abundant in samples collected 14-37 days after burning.

In 1980, sustained aerial regrowth appeared on all four

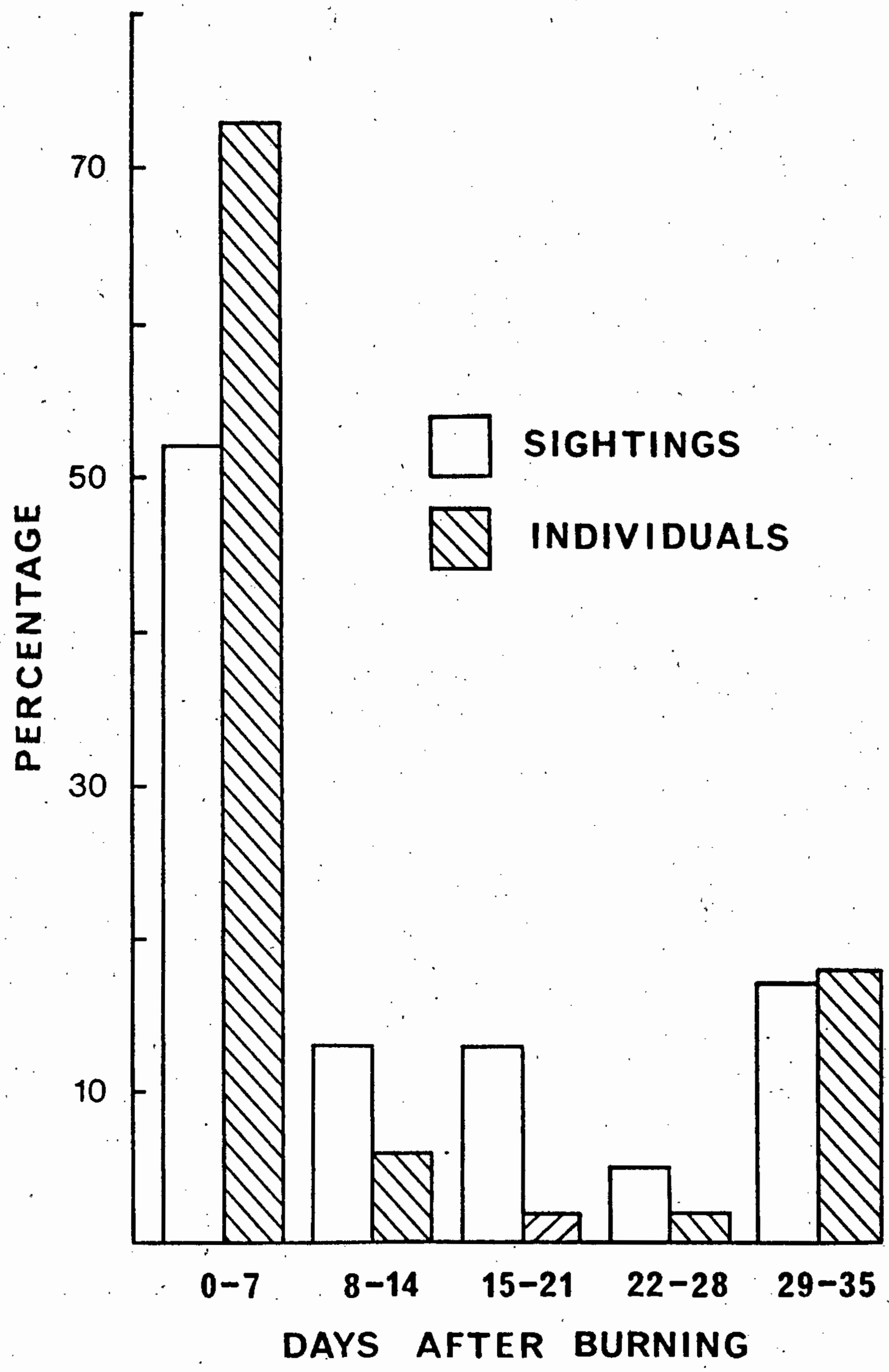

FIG. 2.1 Relative frequency of bald ibises recorded feeding in winter-burnt grassland during June-August in 1978, 1979 and 1980, in relation to the time elapsed after burning, based on 23 sightings and 180 individuals.

firebreaks in mid-August, *ca* 36-70 days after burning. Samples collected after the resumption of sustained aerial growth indicate a concommitant increase in the abundance of live invertebrates in winter-burnt grassland to levels exceeding those obtained during the initial week after burning (Table 2.2).

TABLE 2.1 : Arthropods collected in 12 sampling trials on four different firebreaks on the farm "Durleigh" during June-August 1980. Total specimens = 164.

Taxon	Alive	Dead	Percent Total Specimens	Frequency in Sampling trials (%)
Orthoptera				
Acrididae	53	39	56,10	75,0
Tetrigidae	0	1	0,61	8,3
Tettigoniidae	2	1	1,83	16,7
Blattidae	8	1	5,49	66,7
Coleoptera				
Curculionidae	2	3	3,05	33,3
Scarabeidae	0	8	4,88	41,7
Tenebrionidae	0	1	0,61	8,3
Homoptera				
Cicadellidae	1	1	1,22	16,7
Hemiptera				
Coreidae	0	1	0,61	8.3
Reduviidae	0	1	0,61	8,3
Pentatomidae	4	1	3,05	25,0
Lepidoptera				
larvae	5	8	7,92	33,3
pupae	0	1	0,61	8,3
Hymenoptera				
wasp	0	1	0,61	8,3
Isoptera	0	1	0,61	8,3
Spider	18	0	10,97	33,3
Tick	0	1	0,61	8,3
Centipede	0	1	0,61	8,3

<u>TABLE 2.2</u> : Abundance of living and dead arthropods collected in 360 samples in winter-burnt grassland in relation to time elapsed after burning.

Days elapsed after burning	Total Samples	Number of Arthropods Collected	
		Alive	Dead
dormant grassland:			
0-7	120	31	61
14-37	120	12	6
post-burn regrowth:			
46-82	120	50	4

2.5 Discussion

The feeding habits of *G. calvus* are poorly known, and no systematic study of its diet has been made, although insects, earthworms, snails and small vertebrates are probably the main food items consumed by bald ibises (Layard & Sharpe 1875-1884, Stark & Sclater 1906, Roberts 1940, Vincent & Symons 1948), reflecting a range in diet similar to that recorded in the closely related waldrapp or red-cheeked ibis *G. eremita* of Turkey and Morocco (Smith 1970, Cramp & Simmons 1977, Hirsch 1979). Although no observations were made on the selectivity of particular prey items by foraging bald ibises, the results of sampling macrofauna in winter-burnt grassland suggest that acridids, spiders, Coleoptera, lepidopterous larvae and blattids compose the bulk of food items consumed by *G. calvus* in the study area during winter, when most sightings of foraging bald ibises were recorded in burnt grassland (Manry 1982).

Observations on bald ibises foraging in dormant, winter-burnt grassland for which the date of burning was determined indicate that the birds feed in burnt grassland mainly during the initial week after burning, but continue to visit burnt areas for at least five weeks after burning. Sampling of macrofauna indicate that living and dead arthropods are most abundant in dormant, winter-burnt grassland 0-7 days after burning, but occur in reduced numbers 14-37 days after burning, although dead arthropods in particular are substantially less abundant in dormant burnt grassland following the initial week after burning.

The primary advantage for bald ibises feeding in recently burnt grassland, compared to older burnt areas, may be the abundance of dead prey items killed by the fire. Arthropods killed in grass-fires are little damaged except for scorching and slight charring of extremities. Living and dead arthropods are easier to locate in burnt grassland, where most vegetation has been removed by the fire, and once located, dead prey items require no further pursuit. Moreover, invertebrates fleeing ahead of the fire may accumlate in front of the advancing flame front and be overtaken, leaving rich concentrations of dead prey items which are dispersed patchily on the firebreak. Upon landing on a firebreak bald ibises usually move uni-directionally across the burnt area as a swarm, or in a row, with each bird maintaining a regular distance of *ca* 0,4-1,5 m from its nearest companion on either side. Bald ibises walk rapidly over burnt grassland and probe the ground on either side of the search path, picking up food items from the surface and pausing occasionally to probe into the soil. Birds that lag behind the formation to feed where prey items are concentrated soon attract other ibises to their vicinity. In these circumstances bald ibises seemed tolerant of conspecifics feeding closeby, and occasionally two or three birds were observed probing simultaneously in a <0,01 m² area without showing signs of aggression. The bald ibis' group foraging behaviour, involving systematic ground-search formations and mutual tolerance of conspecifics feeding very closeby, seems well suited to locating and exploiting localised concentrations of food in burnt areas.

An additional advantage to foraging in burnt grassland is the conspicuous appearance of burnt areas against the surrounding unburnt grass, so that they can be located easily from an aerial vantage point. Bald ibises utilise rising air currents to gain altitude with little expenditure of energy. Birds ascending on a thermal or updraught circle in a compact flock in a manner similar to migrating flocks of *Buteo* buzzards and other raptorial birds. After reaching a certain height the birds glide in a shallow descent to intercept the ground several kilometres away.

The means by which bald ibises distinguish recently-burnt grassland from older burns are not known, although two possible methods seem plausible. First, birds may detect a grassfire from a considerable distance away by noticing the rising smoke column and flying toward it. After locating a burnt area, an ibis may return to it to feed on subsequent days, perhaps accompanied by other birds that were previously unaware of its position. Secondly, bald ibises may use colour as an indicator of the burn's age. Recently-burnt grassland is dark black, but its colour fades gradually as the ash is dispersed by wind. Human investigators estimate the ages of burnt areas appearing in satellite imagery by referring to a grey scale (Jarman 1973). Similarly, *G. calvus* may also distinguish recent from older burnt areas by their degree of blackness.

The abundance of living and dead arthropods on a firebreak immediately after the fire will depend partly on the numbers present at the time of burning, the nature of the vegetation and terrain, as well as the type, intensity and rate of spread of the fire. Highly mobile invertebrates flee into the surrounding unburnt vegetation, while other take refuge in rocks, termitaria, burrows, cracks in the ground and islands of unburnt vegetation, and may re-occupy the burnt area later. Subterranean forms are generally unaffected by fire *per se*, but may be adversely affected by the post-fire environment (Rice 1932, Cancelado & Yonke 1970, Gillon 1972, Lamotte 1975, Frost in press). The rate at which the numbers of living and fire-killed invertebrates diminish on a firebreak after burning will depend partly on local decomposition rates, and the presence of predators and scavengers.

Shortly after the renewal of aerial growth in burnt grassland between mid-July and mid-August, *G. calvus* adjusts its winter foraging strategy, which emphasises feeding in recently burnt grassland, to include older burnt areas supporting short, post-burn regrowth (Manry 1982). Several studies conducted in grassland and savanna areas in North America and tropical Africa show that invertebrates begin to increase in numbers in burnt vegetation shortly after the renewal of aerial growth, and that the abundance of invertebrates in post-burn regrowth may exceed that obtained in adjacent, unburnt vegetation (Rice 1932, Tester & Marshall 1961, Cancelado & Yonke 1970, Gillon 1972, Lamotte 1975). In the present study an increase in arthropod numbers was apparent *ca* 10-14 days after the appearance of new growth. Thus, old winter-burnt grassland may become a highly profitable habitat type for foraging bald ibises shortly after the renewal of aerial growth in late winter.

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CHAPTER 3

REPRODUCTIVE PERFORMANCE OF THE BALD IBIS IN RELATION TO RAINFALL AND GRASS-BURNING

3.1 Introduction

The bald ibis *Geronticus calvus* is a rare species endemic to the southeastern highlands of southern Africa. Like its sole congenor, the waldrapp or red-cheeked ibis *G. eremita* of North Africa and the Middle East, the bald ibis breeds colonially on high, vertical cliffs, feeds in flocks and congregates in communal roosts (Siegfried 1971).

The bald ibis is primarily an insectivore, and feeds mainly in indigenous grassland and in cultivated areas. The grasslands frequented by the bald ibis are subject to annual burning, and the species feeds extensively in burnt grassland and in short, post-burn regrowth during the annual prescribed grass-burning season (Manry 1982). This paper documents annual variation in the reproductive effort and success of bald ibises during three consecutive breeding seasons (1978-80) at a single breeding colony in Natal, South Africa, and discusses the reproductive performance of bald ibises, and their use of foraging habitat, in relation to rainfall and grass-burning.

3.2 Study area and grass-burning

The study area is in western Natal, South Africa (Manry 1982). Altitude ranges between 950 and 1 950 m above sea level, mean annual rainfall varies between 600 and 1 000 mm, and ambient temperature ranges from -13,3 to 45,0°C (Edwards 1967). The vegetation consists mainly of indigenous grassland and savanna-woodland. Approximately 26% of the study area is under cultivation, silviculture and non-agricultural forms of land-use. Maize *Zea mays* and pastures (Italian ryegrass *Lolium multiflorum*, Kikuyu grass *Pennisetum clandestinum*, lovegrass *Eragrostis curvula* and lucerne *Medicago sativa*) are important foraging habitats for bald ibises (Manry 1982). Grassland in the study area is a sub-climax community maintained by periodic burning. Two forms of prescribed burning are practised in the study area, viz. firebreak burning and spring burning (Manry 1982). Firebreak burning involves firing grassland in strips (usually between 10 and 100 m wide) to create a network of firebreaks for protection against runaway grassfires. Firebreaks are usually burnt during May-July, with a majority burnt in June. Spring burning consists of firing extensive areas of grassland, primarily to eliminate old, moribund foliage and to stimulate new growth for domestic livestock (Scott 1951, 1955).

3.3 Methods

3.3.1 Nesting of bald ibises

Nesting of bald ibises was observed at a breeding colony situated on cliffs surrounding a 39 m high waterfall on the Mooi River, approximately 42 km WSW of Greytown, Natal, South Africa. Nesting sites were on open ledges, and each site was inspected at one-to-seven-day intervals, from the onset of nesting in late July or early August, until the last nestlings fledged (i.e., vacated the nesting ledge for the first time under their own powers of flight) or expired in December. Observations were aided by 8 x 35 binoculars, often supplemented with a 15-60 x zoom telescope, and were entered into notebooks.

Out of a total of 60 nesting sites used by bald ibises in the study colony during 1978-80, 22 were favourably situated so as to allow inspection of nest contents from three different hides situated above the nesting cliffs. Adult birds occupying these focal nesting sites were recognised individually by the distinctive patterns of grooves and depressions on their hard, naked crowns, which were sketched and photographed. Recognition and documentation of the diagnostic head pattern characteristics of individual birds were improved and extended to include more birds in 1979 than in 1978, so that in 1980, more birds were recognised from the previous breeding season than in 1979.

Clutch-size, hatching success, nestling survival and fledging success were monitored in focal nesting sites. In the remaining nesting sites, the number of eggs and small nestlings could not be established with certainty, and only the number of nestlings raised to fledging age (i.e., 40-45 days after hatching) could be determined. Breeding at sites where the nest contents could not be observed was indicated by the onset of incubation behaviour in the resident pair. The nesting period at the study site (31 July-30 December) was divided into 23 seven-day intervals (beginning with 30 July $\pm$ 3 days) to facilitate comparisons between years.

The number of bald ibises residing in the colony was determined at frequent intervals by counting the birds as they departed for feeding areas in the early morning. Birds remaining in the colony after the morning exodus were then counted, and their number, added to the count of those departing, yielded a complete census of the colony.

3.3.2 Habitat use by foraging bald ibises

All sightings of bald ibises foraging in the study area were recorded, and the following details were noted: date, time of day, locality, number of ibises present, vegetation type, foliage height and weather conditions. Vegetation was classified as one of five basic types, viz. grassland, cultivated pastures, maize fields, ploughed fields and abandoned cultivation. Five different grassland "forms" were distinguished according to foliage height and stage of recovery from burning, i.e. burnt grassland with no sustained regrowth, patchy post-burn regrowth, uniform short growth (<70 mm tall), medium growth (70-120 mm tall); and tall growth (> 120 mm tall). The last three categories include grass recovering from burning as well as unburnt grass shortened by grazing and mowing (Manry 1982).

3.3.3 Rainfall

Daily measurements of rainfall were recorded at Weston Agricultural College, Mooi River (29° 13'S, 30° 02'E, 1493 m above sea level), and were provided through the courtesy of the Agrometerological Section, Cedara College, Natal.

3.4 Results

3.4.1 Reproductive performance of bald ibises

3.4.1.1 Nesting chronology and colony population

The timing of egg-laying, hatching of eggs and fledging of nestlings was remarkably similar in all three years (Fig. 3.1). The first clutch of the season was initiated between 31 July and 5 August, while the final clutch of the season was initiated between 19 and 20 October. The first fledglings vacated their nesting ledges on 17 October in both 1978 and 1979, and on 14 October in 1980. The last nestling in the colony fledged on 22 and 30 December in 1978 and 1979, respectively. In 1980, the last nestlings to fledge vacated their nesting ledge on 26 November, while two additional nestlings remained in the colony until 10 December, when they were swept from their nesting site by floodwaters of the Mooi River.

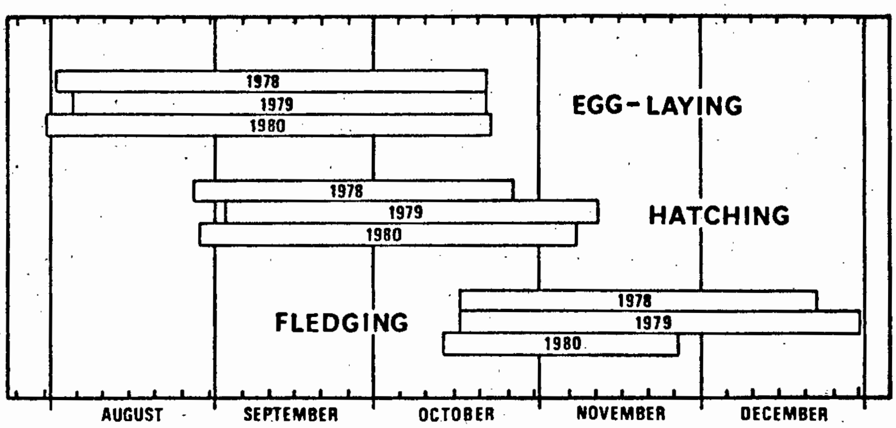

FIG. 3.1 Timing of egg-laying, hatching and fledging of nestlings at the study colony during 1978-80.

A mean clutch-initiation time ($\bar{T}$) was calculated for each year using a modified version of Cavé's (1968) formula:

$$\bar{T} = \frac{\Sigma(T \times N)}{\Sigma N}$$

where T is the number of days elapsed since 26 July (in seven-day increments), and N is the number of nests initiated in each seven-day interval. The values of $\bar{T}$ and mean clutch-initiation dates ($\bar{C}$) for each year are given in Table 3.1. The mean clutch-initiation date was similar in 1978 and 1979, but was six-to-seven days earlier in 1980. This is owing partly to the relative lack of re-nesting attempts by pairs that failed in their primary attempt in 1980, compared to 1978 and 1979 (Table 3.2), which constituted a majority of clutches laid after 13 September (Fig. 3.2).

The number of ibises residing in the study colony during the egg-laying period increased from 98-108 in 1978, to 120-148 in 1980 (Table 3.3).

3.4.1.2 Clutch-size

The distribution of clutch-size, and the mean size of 61 clutches during 1978-1980 are shown in Table 3.4. This sample excludes nine replacement clutches laid by pairs that failed in their initial breeding attempt. All primary clutches consisted of two (c/2) or three (c/3) eggs. The mean clutch-size was almost identical in 1978 and 1979, but was substantially smaller in 1980, as a result of fewer c/3 clutches in that year (Table 3.4).

The sizes of primary clutches laid by 13 individually

TABLE 3.1 : Calculation of mean clutch initiation dates ($\bar{C}$) at the study site during 1978-80 (see text).

	$\Sigma(T \times N)$	ΣN	$\bar{T}$	$\bar{C}$
1978	2037	58	35,1	30 August
1979	1848	55	33,6	29 August
1980	1183	43	27,5	23 August

TABLE 3.2 : Success of breeding attempts in focal nesting sites during 1978-80.

	1978	1979	1980
Number of pairs breeding in focal sites	21	20	20
Number of initial breeding attempts that fail	8	6	9
Number of re-nesting attempts	5	3	1
Total nesting attempts	26	23	21
Per cent clutches in which 1-3 eggs hatch successfully[a]	73,1	78,3	76,2
Per cent broods in which 1-2 hatchlings reach fledging age[b]	78,9	83,3	68,8
Per cent nesting attempts producing at least one fledgling[c]	57,7	65,2	52,4
Per cent breeding pairs producing at least one fledgling[d]	71,4	75,0	55,0
Mean number of fledglings per nesting attempt[e]	0,89	0,96	0,57
Mean number of fledglings per breeding pair[f]	1,10	1,10	0,60

Notes: [a]NS (not significant) (χ^2 = 0,18, df = 2; P > 0,50).

[b]NS (Fisher's Exact Test, P > 0,50).

[c]NS (χ^2 = 0,76, df = 2; P > 0,50).

[d]NS (χ^2 = 2,07, df = 2;0,50 > P > 0,25).

[e]NS (χ^2 = 6,14, df = 4;0,25 > P > 0,10).

[f]NS (χ^2 = 7,25, df = 4;0,25 > P > 0,10).

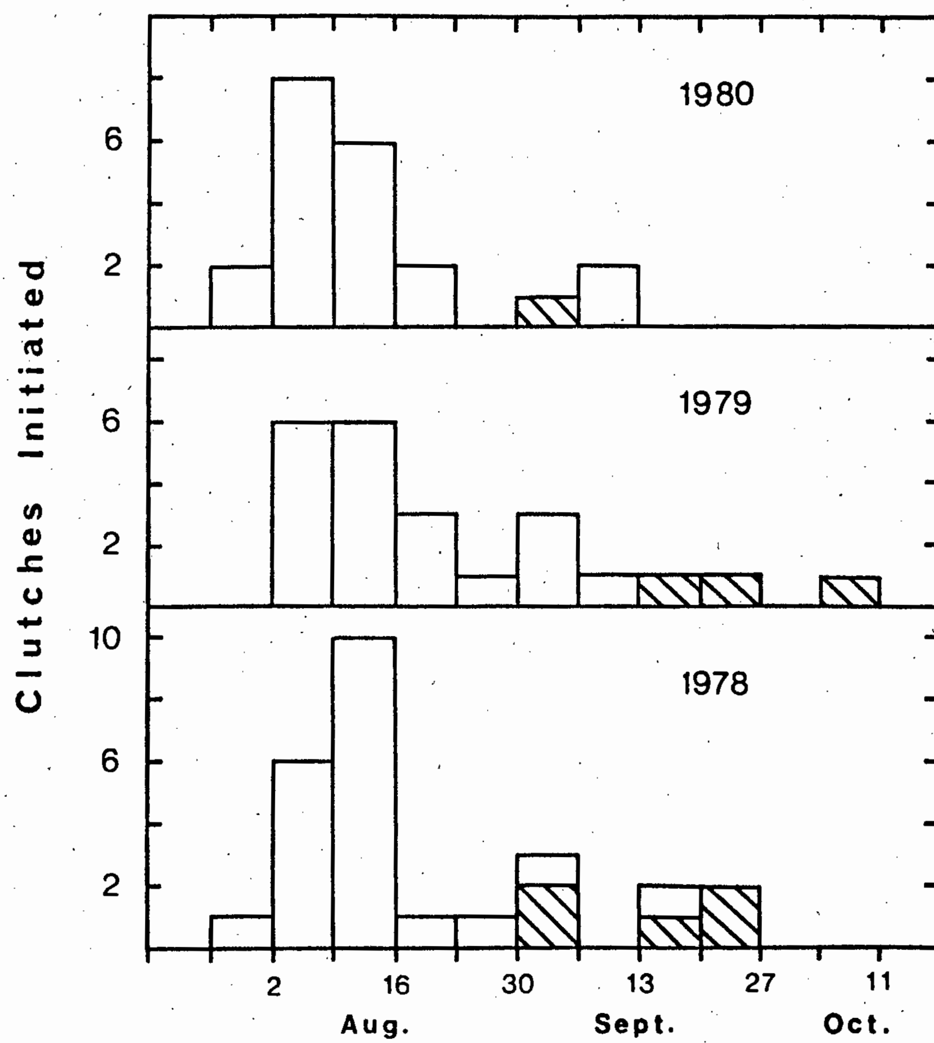

FIG. 3.2 Numbers of primary (clear columns) and replacement (hatched columns) clutches initiated in focal nesting sights per seven-day interval of the breeding period in 1978-80.

TABLE 3.3 : Approximate numbers of ibises residing at the breeding colony during the onset (1-5 August), mean date C (23-30 August, see Table 3.1) and final day (19-22 October) of the egg-laying period in 1978-80.

Date	1978	1979	1980
1-5 August	98	120	120
23-30 August	100	117	127
19-22 October	108	124	148

TABLE 3.4 : Distribution of clutch-size, and mean clutch-size in 61 primary nesting attempts in focal nesting sites during 1978-80.

	Clutch-size (eggs)[a]		
Year	2	3	Mean clutch-size
1978	16	5	2,24
1979	15	5	2,25
1980	19	1	2,05
Cumulative	50	11	2,18

Note: [a]Distribution of clutch-sizes not significantly different between years (Fisher's Exact Test, $P > 0,10$).

recognised females breeding in focal nesting sites in two or three consecutive years are shown in Table 3.5. Of six females for which primary clutch-size was determined in all three years, three laid c/2 clutches in each year, whereas the remainder laid two c/2 clutches and one c/3 clutch. In 11 females observed in both 1979 and 1980 (Table 3.5), the mean clutch-size was reduced from 2,27 in 1979, to 2,09 in 1980.

3.4.1.3 Breeding success of focal pairs

The number of pairs breeding (i.e., initiating a clutch of eggs) in focal nesting sites in all three years varied by one (Table 3.2). Whereas 15 breeding pairs produced at least one fledgling in 1978 and 1979, only 11 pairs succeeded to do so in 1980. The mean number of fledglings produced per breeding pair in 1978 and 1979 was identical, but was substantially lower in 1980 (Table 3.2).

A total of 70 focal breeding attempts (including nine re-nesting attempts) was monitored during 1978-80 (Table 3.2). Survival of clutches during the pre-hatching stage was similar in all three years (73-78%). Brood survival during the nestling stage was substantially lower in 1980 than in 1978 and 1979. Consequently, the proportion of breeding attempts resulting in fledged offspring, and the mean number of fledglings produced per breeding attempt, were lower in 1980 than in 1978 and 1979 (Table 3.2).

The fate of 148 eggs laid in 70 clutches was monitored (this sample includes two replacement clutches that disappeared during the egg-laying stage) (Table 3.6). Fewer eggs were laid in 1980, compared to 1978 and 1979, but hatching success of eggs was higher in 1980 than in the two previous years, so that the mean hatchling brood-size was correspondingly higher in 1980, compared to 1978 and 1979 (Table 3.7). However, mortality of nestlings was

TABLE 3.5 : Clutch-sizes laid by individual females in focal nesting sites during 1978-80.

Female No.	Clutch-size in year		
	1978	1979	1980
1	2	3	2
2	2	3	2
3	2	2	2
4	2	2	2
5	2	2	2
6	3	2	2
7	2	2	-
8	2	2	-
9	-	2	2
10	-	2	2
11	-	2	3
12	-	3	2
13	-	2	2

TABLE 3.6 : Success of eggs laid in 70 primary and replacement clutches in focal nesting sites during 1978-80.

	1978	1979	1980
Total eggs laid	56	49	43
Per cent eggs hatching[a]	60,7	69,4	72,1
Per cent hatchlings fledged[b]	67,6	64,7	38,7
Per cent eggs resulting in fledged offspring[c]	41,1	45,0	27,9
Total nestlings fledged	23	22	12

Notes: [a]NS (χ^2 = 1,63, df = 2;0,50 P > 0,25).

[b]Statistically significant (χ^2 = 6,64, df = 2; P < 0,05).

[c]NS (χ^2 = 3,04, df = 2;0,25 > P > 0,10).

TABLE 3.7 : Brood-size distribution and mean brood-size at hatching in primary and replacement clutches in focal nesting sites during 1978-80.

	Brood-size (hatchlings)[a]			
Year	1	2	3	Mean brood-size
1978	6	11	2	1,79
1979	6	8	4	1,89
1980	2	13	1	1,94
Cumulative	14	32	7	1,87

Note: [a]Distribution of hatchling brood-sizes not significantly different between years (χ^2 = 5,42, df = 4; 0,25 > P > 0,10).

substantially higher in 1980, so that comparatively fewer eggs resulted in fledged offspring in that year (Table 3.6). Furthermore, the mean fledgling brood-size was lowest in 1980, owing largely to the fact that only one pair produced two fledglings in that year, compared to eight and seven pairs that succeeded in doing so in 1978 and 1979, respectively (Table 3.8).

In addition to lower overall reproductive success, fewer pairs that failed in their primary breeding attempt proceeded to lay a replacement clutch in 1980, compared to 1978 and 1979 (Table 3.2). Furthermore, one pair that nested on the same ledge in 1978 and 1979 did not attempt to breed in 1980, even though they occupied their nesting site daily throughout the full duration of the nesting period, and often gathered and arranged sticks, grass and other materials to construct incomplete nests.

3.4.1.4 Breeding success of the colony as a whole

Breeding success of the colony as a whole (Table 3.9) was lower in all comparisons than in the focal sample (Table 3.2), owing to the position of 10 non-focal nesting sites close to the cascading waterfall. These sites were susceptible to inundation when the river flooded after heavy rains, and consequently suffered the highest failure rates of the entire colony. Thus, reproductive performance in the focal nesting sites was not fully representative of the colony as a whole.

Fewer breeding attempts were initiated in 1980, compared to 1978 and 1979 (Table 3.9). Furthermore, the proportion of breeding attempts resulting in fledged offspring, and the number of fledglings produced per breeding attempt, were similar in 1978 and 1979, but were substantially lower in 1980 (Table 3.9). Mean fledging brood-size was substantially lower in 1980 than in the two previous years; only

TABLE 3.8 : Brood-size distribution and mean brood-size at fledging in primary and re-nesting attempts in focal nesting sites during 1978-80.

	Brood-size (fledglings)[a]		
Year	1	2	Mean brood-size
1978	7	8	1,53
1979	8	7	1,47
1980	10	1	1,09
Cumulative	25	16	1,39

Note: [a]Distribution of fledging brood-sizes not significantly different between years (χ^2 = 5,80, df = 2; 0,10 > P > 0,05).

TABLE 3.9 : Breeding success of all nesting attempts in the study colony during 1978-80.

	1978	1979	1980
Total number of nesting attempts	58	55	43
Per cent nesting attempts that produce fledged offspring [a]	43,1	47,3	32,6
Total number of fledglings produced	36	37	16
Mean number of fledglings produced per nesting attempt [b]	0,62	0,67	0,37

Notes: [a] NS (χ^2 = 2,23, df = 2; $0,50 > P > 0,25$).
[b] NS (χ^2 = 5,56, df = 4; $0,25 > P > 0,10$).

two pairs succeeded in raising two offspring to fledging age in 1980, compared to 11 pairs that succeeded in doing so in 1978 and 1979 (Table 3.10).

3.4.2 Rainfall, grass-burning and habitat use by foraging bald ibises

Mean monthly rainfall, and monthly rainfall recorded from July 1977 to June 1981 at Weston College, are shown in Fig. 3.3. Approximately 80% of the mean annual rainfall occurs during October-March, with a peak in summer (December-February). Thus, the total rainfall received during a calendar year (January-December) includes precipitation from two consecutive annual rainfall cycles. For this reason, monthly rainfall totals are summed over the period July-June (herein called a "twelve-month"), which encompasses a single annual rainfall cycle. Furthermore, July-June represents the 12-month period preceding the first month of breeding at the study colony.

Total rainfall during the 1977/78 and 1978/79 twelve-months (preceding the 1978 and 1979 breeding seasons, respectively) amounted to 150% and 140%, respectively, of the annual mean of 702 mm, whereas the 1979/80 twelve-month received only 76% of the mean total twelve-month rainfall calculated for the period July 1928-June 1981 (Fig. 3.3). Moreover, the sub-average rainfall received in 1979/80 was closer to the 53-year mean value than the exceptionally high rainfall totals of 1977/78 and 1978/79.

Spring grass-burning is normally confined to August-October (Manry 1982), although the timing and extent of spring grass-burning vary annually according to the amount and distribution of rainfall prior to and during the prescribed burning season. In 1978, substantial rains did not fall until late August (Fig. 3.3), and spring grass-burning began in the study area on 25 August. Total rainfall was above average

TABLE 3.10 : Brood-size distribution, and mean brood-size at fledging in all nesting sites during 1978-80.

Year	Brood-size (fledglings)[a]		Mean brood-size
	1	2	
1978	14	11	1,44
1979	15	11	1,42
1980	12	2	1,14
Cumulative	41	24	1,37

Note: [a]Distribution of fledgling brood-sizes not significantly different between years ($\chi^2 = 3{,}94$, df = 2, $0{,}25 > P > 0{,}10$).

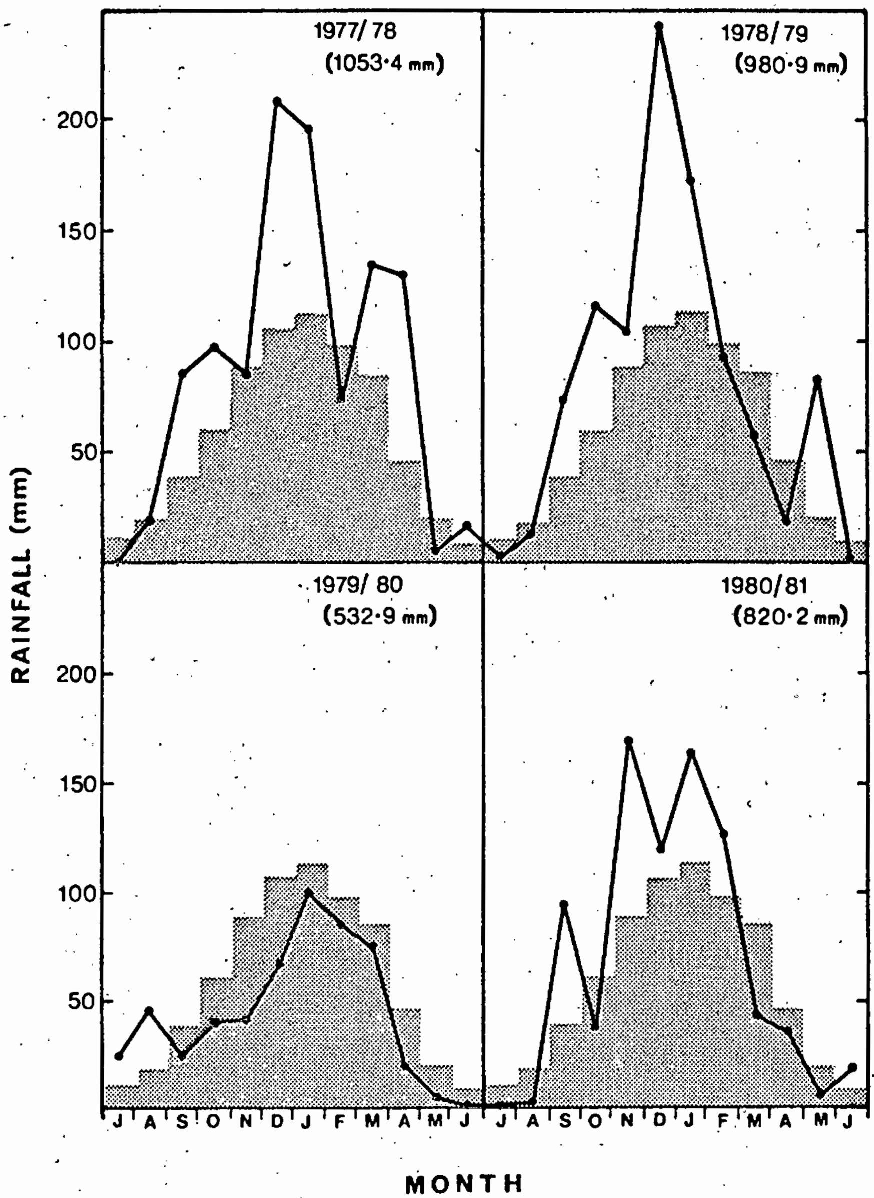

FIG. 3.3 Mean monthly rainfall (shaded columns) and monthly rainfall recorded at Weston College, Mooi River, Natal from July 1977 to June 1981. Twelve-month (July-June) rainfall totals are given in parentheses. Mean monthly rainfall based on continuous records from July 1928 to June 1981 (53 years).

during August-October 1978 (Fig. 3.3), and extensive areas of grassland were burnt, primarily in September and early October. In 1979, early rains in mid-July stimulated the appearance of lush regrowth as early as 23 July, and large areas of grassland were burnt primarily in August and early September. Thus, spring grassland burning was initiated and completed approximately one month earlier in 1979, compared to 1978. By August 1980, following on 11 consecutive months of sub-average rainfall (Fig. 3.3), the soil moisture content was severly depleted. Removal of the grass cover by burning hastens water loss through run-off and evaporation, and grass-burning during a severe drought causes considerable harm to grasses (Cook 1939, Scott 1951, 1955, Daubenmire 1968), so few landowners burnt grass in 1980. After abundant rains fell in September and October in 1980 (Fig. 3.3), a few relatively small areas of grassland were burnt, but most landowners abstained from grass-burning in that year.

Figures 3.4-3.6 illustrate the influence of grass-burning on the selection of habitat by foraging bald ibises. During June-July of 1979 and 1980, most birds were recorded feeding in burnt grassland on firebreaks, with pastures and maize fields being of lesser importance (Fig. 3.4). The amount of rainfall received during June-July in both years differed considerably (Fig. 3.3), but rainfall has little effect on the timing and extent of firebreak burning. This is reflected in the similarity of the relative use of different habitats by foraging bald ibises observed during June-July in both years (Fig. 3.4).

Although a similar number of observations was obtained during August-September in both 1979 and 1980, the use of habitat by foraging bald ibises during this period differed markedly between both years (Fig. 3.5). Following the early commencement of spring grass-burning in July 1979, large areas of burnt grassland and short, post-burn regrowth were available during August-September, which were utilised

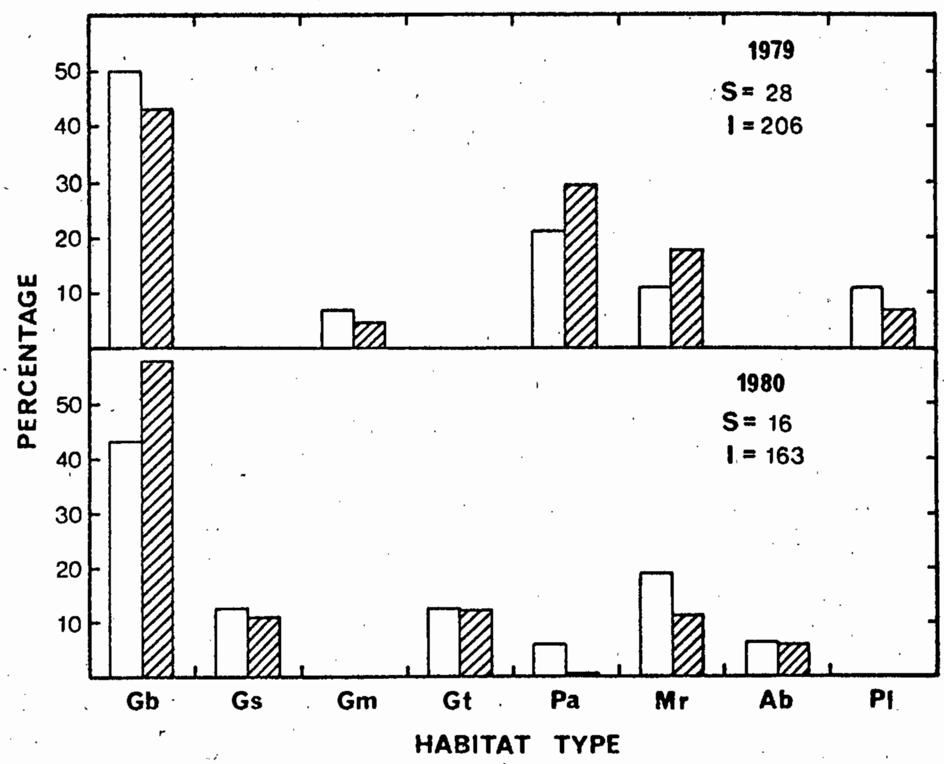

FIG. 3.4 Proportion of sightings (clear columns) and total individuals (hatched columns) recorded foraging in different habitat types during June-July in 1979 and 1980. "S" and "I" designate the number of sightings and total individuals, respectively, observed foraging in all habitat types during each two-month period. Habitat types are designated Gb (burnt grassland), Gp (patchy post-burn regrowth), Gs (short grassland), Gm (medium grassland), Gt (tall grassland), Pa (pastures), Mr (reaped maize fields), Ab (abandoned cultivation), Pl (ploughed fields).

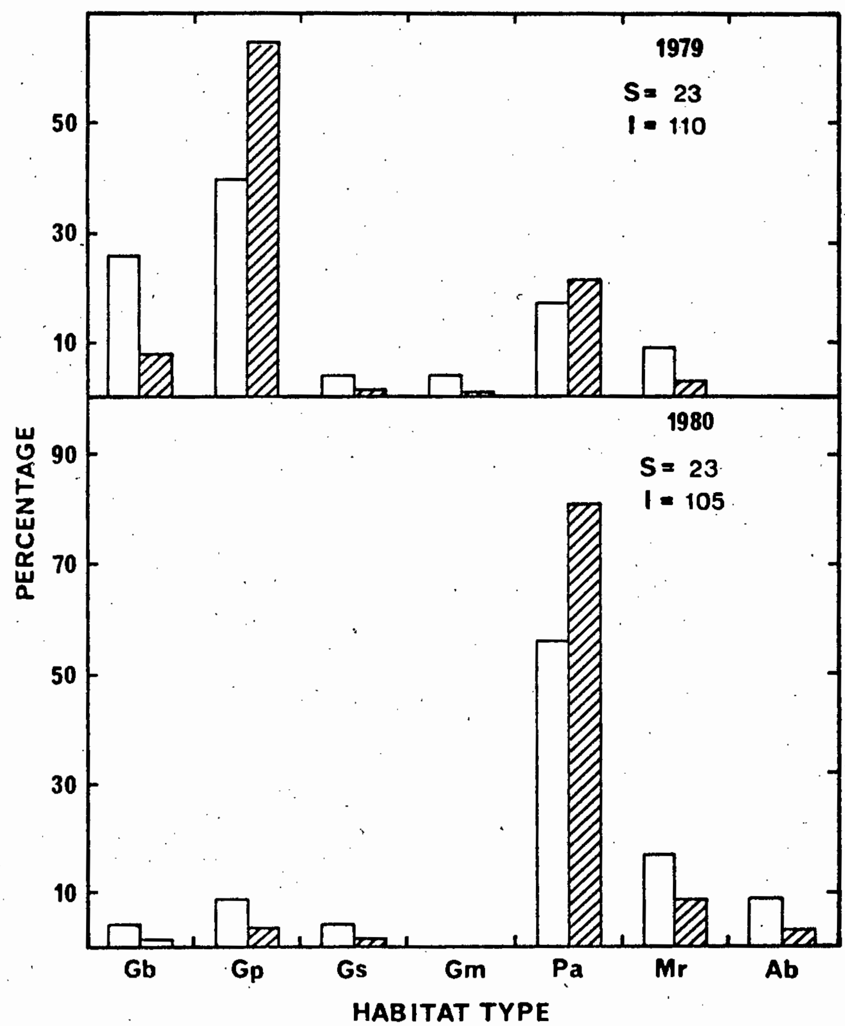

FIG. 3.5 Proportion of sightings and total individuals recorded foraging in different habitat types during August-September in 1979 and 1980. See Fig. 3.4 for conventions.

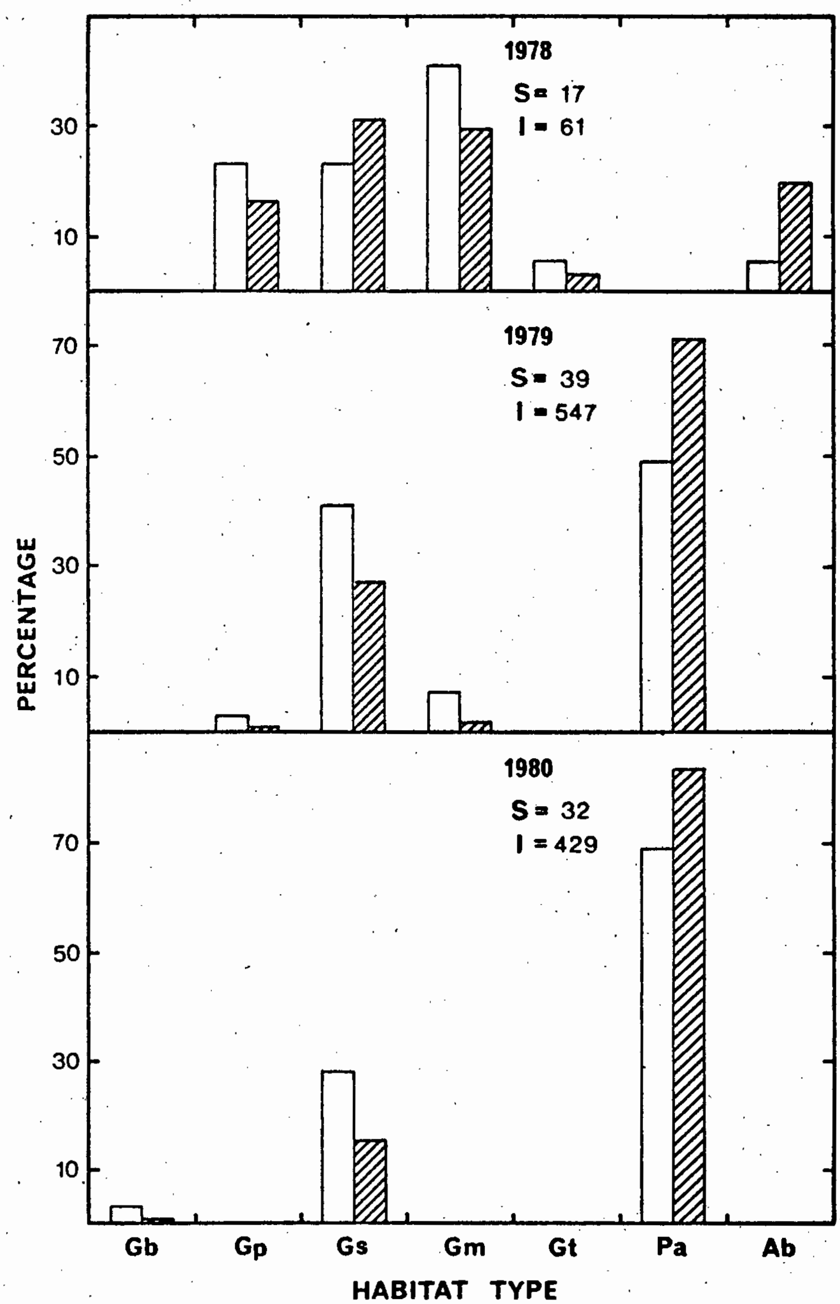

FIG. 3.6 Proportion of sightings and total individuals recorded foraging in different habitat types during October-November in 1978, 1979 and 1980. See Fig. 3.4 for conventions.

extensively by foraging bald ibises (Fig. 3.5). By contrast, with the delayed onset and lesser extent of spring grass-burning in 1980, few ibises were recorded feeding in burnt grassland and post-burn regrowth during August-September, and a majority of records was from cultivated pastures (Fig. 3.5).

Data on habitat use by foraging bald ibises during October-November 1978 are compared with the results from the same period in 1979 and 1980 (Fig. 3.6). No sightings were made in cultivated pastures during October-November 1978, and post-burn regrowth (patchy, short and medium height) was the habitat type used most extensively by foraging bald ibises during that period (Fig. 3.6). By contrast, most foraging ibises observed during October-November were recorded in cultivated pastures in both 1979 and 1980, while short grass was used less frequently (Fig. 3.6). The low proportion of birds observed feeding in short post-burn regrowth during October-November 1979, compared to the same period in 1978, was probably due to the relatively early commencement of grass-burning, and the rapid regrowth of grass in burnt areas in 1979 - most spring-burnt grassland was covered in tall, dense foliage by October. The proportion of ibises observed feeding in cultivated pastures during October-November 1980 (Fig. 3.6) was similar to that observed in the two previous months in the same year (Fig. 3.5).

3.5 Discussion

The reproductive performance of bald ibises at the study colony was remarkably similar in the wet years of 1978 and 1979, but was substantially reduced in the relatively dry year of 1980. Fewer females laid c/3 clutches in 1980, compared to the two previous years, resulting in a lower mean clutch-size in that year, and at least one pair that bred in 1978 and 1979 failed to breed in 1980. In 1980, fewer breeding pairs produced fledged offspring, and mean brood-size at fledging was smaller, compared to 1978 and 1979.

Reduced breeding, or abstinence from breeding, and low reproductive success during droughts have been reported for a number of avian species, including five species of ibises, and explained by the effects of rainfall on the birds' food supply (Lack 1954, Carrick 1962, Kahl 1964, Brenner 1966, Ryder 1967, Klomp 1970, Robin 1973, Kushlan 1974). For the bald ibis, two explanations seem plausible. First, arthropods and other terrestrial invertebrates are generally less abundant in drought years than in years with normal or above-average rainfall (Ellstrom 1974, Kemp 1976, Earlé 1981), and the low rainfall received during the 1979/80 twelve-month probably created a shortage of prey for bald ibises immediately prior to and during the 1980 breeding season. Secondly, the shortage of burnt grassland in 1980, also a result of low rainfall, forced the birds to seek alternative habitat types to forage in, primarily cultivated pastures. Burnt grassland and post-burn regrowth manifest several distinct characteristics which might make them more profitable as foraging habitats for bald ibises than available alternatives (Manry 1982). Moreover, cultivated pastures occupy approximately six per cent of the study area, whereas spring grass-burning may involve between 20 and 45 per cent of the total area of grassland in a favourable year (Manry 1982). Thus, the ibises encountered a shortage of their preferred foraging habitat during the 1980 breeding season, which may have contributed to the lowering of their reproductive performance in that year. Unfortunately, the relative effects of variations in prey abundance and the extent of optimal foraging habitats on the reproductive performance of bald ibises cannot be evaluated separately, as both co-operate to determine the availability of food for the birds.

Food availability may affect clutch-size in birds through its effects on the physical condition of the female, so that when food is in short supply, breeding females are metabolically incapable of producing the maximum clutch-size, and so lay smaller clutches (i.e., the "direct" effect of food supply on clutch-size: Klomp 1970). Alternatively, food shortage prior to or during the egg-laying period may activate an adaptive response whereby females lay smaller clutches than what their physical condition would enable at the time, so that relatively more food is available for the smaller broods of hatchlings (i.e., the "indirect" effect of food supply on clutch-size: Klomp 1970, also see Bengston 1971).

Distinguishing the direct from the indirect effects of food supply on clutch-size in birds is virtually, if not entirely, impossible in the field (Klomp 1970). However, in the present study, overall hatching success, and mean hatchling brood-size were highest in 1980. Thus, in 1980, the lower mean clutch-size did not result in smaller brood-sizes at hatching (*contra* the indirect effect of food supply on clutch-size discussed by Klomp 1970 and Bengston 1971). A higher nestling mortality rate, due largely to parental nest desertion and, presumably, starvation, accounted for the substantially lower reproductive output in 1980, compared to 1978 and 1979.

Jones & Ward (1976) suggest that the eventual clutch-size in birds is determined by the size of the female's stored protein reserve before and during egg-formation. In the present context, it seems likely that more favourable feeding conditions enabled breeding females to accumulate, on average, larger protein reserves prior to the onset of egg-laying in 1978 and 1979, which enabled a slightly larger proportion of females to lay c/3 clutches, compared to the drought year of 1980. However, for a majority of breeding females, the usual clutch-size of two eggs remained constant in both years.

Annual variations in clutch-size in birds have also been explained by variations in the population density, the mean date of laying and the age structure of the breeding population (Klomp 1970 and references cited therein). The present study was too brief, and the sample sizes too small to provide for meaningful conclusions on the effects of population size and mean laying date on the average clutch-size in bald ibises. The number of ibises residing at the breeding colony during the egg-laying period increased steadily during the three years of the study, and the increase in population from 1979 to 1980 was of a similar order of magnitude as the change from 1978 to 1979, whereas the mean clutch-size was almost identical in 1978 and 1979, but was substantially lower in 1980. Thus, no clear relationship is indicated between the increase in colony population size during the egg-laying period from 1978 to 1980, and the differences in mean clutch-size observed in all three years. However, the possibility of a threshold effect operating between the 1979 and 1980 population levels cannot be disregarded.

The mean clutch initiation date varied by only one day from 1978 to 1979, but was six-to-seven days earlier in 1980. In most avian species in which a relationship between mean laying date and average clutch-size has been established, the latter tends to become smaller as the laying period advances, and tends to be smaller in years in which breeding is delayed (Klomp 1970 and references cited therein). In the present study, all c/3 clutches were laid in the initial three weeks of the *ca* 12-week laying period, so that mean primary clutch-size tended to decline as the laying period progressed. Thus, the smaller average primary clutch-size in 1980 cannot be attributed to delayed egg-laying.

Finally, in most avian species in which age-related differences in clutch-size have been documented, clutch-size tends to increase with increasing age and breeding experience of the female, and mean clutch-size in a series of breeding seasons may vary according to the ratio of young, inexperienced breeders to older, more experienced birds in the breeding population (Klomp 1970 and references cited therein). The effects of age on clutch-size in the bald ibis are not known, and the age composition of the breeding population at the study site could not be determined. However, the decrease in mean primary clutch-size from 1979 to 1980 in 11 females observed breeding in focal nesting sites in both years was of a similar order of magnitude to that observed in the focal sample as a whole, and thus cannot be attributed to a larger proportion of younger, less experienced females in the latter year.

The distributional range of the bald ibis (Siegfried 1971) is confined to the summer rainfall region of southern Africa (Tyson 1978). Periodic droughts are a frequent occurrence in this region (Tyson 1978), and thus are a regular feature of the bald ibis' environment. The relatively low reproductive output of bald ibises in the study colony in 1980 was apparently sustained by food gathered primarily in cultivated pastures. Approximately 24% of the pasturage in the study area is under irrigation (Manry 1982). It seems plausible to speculate that the availability of irrigated pastures as feeding habitats for bald ibises during the breeding season enables the birds to realise higher reproductive outputs during drought years, than would have been attainable prior to the introduction of pastures in the species' distributional range in the late 19th century.

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CHAPTER 4

LITTER, LIGHTNING AND FIRE IN THE SOUTH AFRICAN GRASSLAND BIOME

4.1 Introduction

Fire is an ecological force of great antiquity in the biosphere. Fossil charcoal deposits indicate the occurrence of fires in vegetation long before man evolved (Harris 1958, Komarek 1972), while evidence for human fire-utilisation as early as 550 000 - 750 000 years ago comes from southern Europe and China (Frost in press). Before man developed the ability to apply fire to vegetation, fires were started in vegetation by "natural" ignition agents, e.g. lightning, rock collisions, volcanic eruptions and spontaneous combustion of organic material (Daubenmire 1968, Killick 1963, Vogl 1974, West 1965). Today, lightning is recognised as the most important "natural" source of fire-ignition in vegetation (Komarek 1967, 1972, West 1972).

Ecologists have long recognised the important influence of fire in the origin, maintenance and distribution of terrestrial plant communities (Bayer 1955, Killick 1963, Naveh 1975, Phillips 1930, Sauer 1950 1956, Stewart 1956, West 1951, 1965, 1972). Man-made fires, as well as the artificial control or elimination of fire, have greatly modified existing plant communities, and contributed to the expansion of certain plant communities at the expense of others (Acocks 1964, 1975, Donaldson 1966, Downing 1974, Du Toit 1972, Feely 1980, Galpin 1926, Phillips 1930, Story 1952, Trollope 1978, West 1965, 1972). However, the significance of natural fire-ignition agents, and particularly lightning, in exposing vegetation to fire over evolutionary time has been largely discounted or neglected by plant ecologists (Komarek 1965, 1972), with only a few notable exceptions (e.g. Bayer 1955, Killick 1963, Mount 1969, Vogl 1969).

It has been suggested that the world's extensive, open (i.e. lacking in woody plant components) grasslands owe their existence to recurrent fires (Sauer 1950, 1956; Stewart 1956). Grasslands occur under climatic conditions that are particularly conducive to fires, and the high flammability of grassland fuels, together with the prevalent fire-propagative weather conditions, ensure that periodic fires are "virtually inevitable" in natural grasslands (Bochert 1950, Vogl 1974, Wells 1970). Grassland biota exhibit numerous adaptations that enable them to survive frequent burning, and some forms may actually depend on periodic fires for their existence (Bayer 1955, Daubenmire 1968, Frost in press, Olindo 1972, Tainton 1981a, Tainton & Mentis in press).

The primary objectives of this paper are three-fold. First, the ecology of fire in the South African grassland biome, as defined by Huntley (in press) and Mentis & Huntley (in press), is reviewed briefly, with particular emphasis on the role of fire in the maintenance of grassland communities in South Africa (Section 4.4). Secondly, the regional incidence of lightning over South Africa is examined, and the main factors responsible for the observed distribution of lightning over the Republic are considered. The range of variation in lightning frequency in different classes of South African vegetation is established, in order to ascertain inter- and intra-biome differences in lightning ground-strike potential (Section 4.5). Finally, a discussion follows on the possible role of lightning in the origin, maintenance and distribution of grasslands in South Africa (Section 4.6).

4.2 Methods

4.2.1 Classification of South African vegetation

Acocks' (1975) veld types were assigned to the biomes and sub-groups within biomes described by Huntley (in press), with the following modifications:

(1) Coastal Forest and Thornveld (Veld Type 1) is assigned to the forest biome.

(2) Zululand Thornveld (Veld Type 6) and Lowveld (Veld Type 10) are assigned to the moist savanna sub-group of the savanna biome.

(3) Kalahari Thornveld invaded by Karoo (Veld Type 17), False Thornveld of Eastern Province (Veld Type 21) and Succulent Mountain Scrub (Veld Type 25) are assigned to the arid savanna sub-group of the savanna biome.

(4) Grassland veld types are assigned to "sour", "sweet", "mixed" (including "tall") and "inland mountain" grassland sub-groups according to Acocks' vegetation map in Talbot & Talbot (1960). Ngongoni Veld (Veld Type 5), North-eastern Mountain Sourveld (Veld Type 8), Highland Sourveld and Dohne Sourveld (Veld Type 44) and Ngongoni Veld of Natal Mistbelt (Veld Type 45) are assigned to the sour grassland sub-group. Invasion of Grassveld by *Acacia karroo* (Veld Type 22) and False Upper Karoo (Veld Type 36) are assigned to the sweet grassland sub-group. Transitional *Cymbopogon-Themeda* Veld (Veld Type 49) is assigned to the mixed grassland sub-group. *Danthonia* Mountain Veld replaced by Karoo (Veld Type 42) and Karroid *Danthonia* Mountain Veld (Veld Type 60) are assigned to the inland mountain grassland sub-group.

4.2.2 Lightning ground-strike densities in vegetation

Since 1975, 353 lightning flash counters have been installed in South Africa (including one in Lesotho) by the National Electrical Engineering Research Institute (NEERI) of the South African Council for Scientific and Industrial Research (Fig. 4.1). Flash counters measure the number of lightning

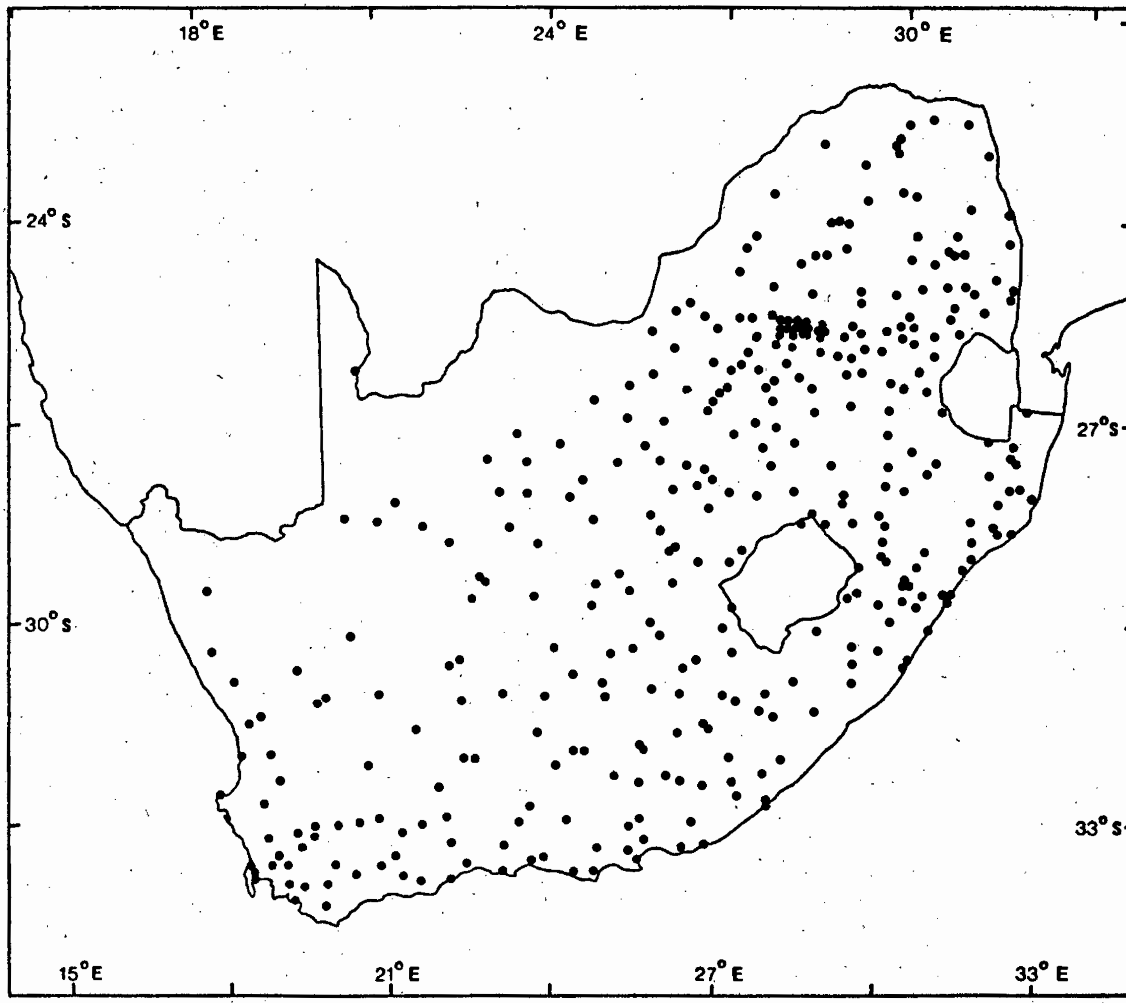

FIG. 4.1 Locations of 353 lightning flash counters operative in South Africa and Lesotho during July 1975-June 1981.

strikes to ground within a *ca* 20 km radius of the counter; details of their design and operation are provided by Anderson *et al.* (1978) and Kröninger (1978, 1981).

For each flash counter, the mean annual lightning ground-strike density (expressed as the average number of strikes·km $^{-2}$·annum $^{-1}$) was calculated from the average number of lightning strikes to ground recorded per annum over the entire period of operation of each counter. These data, together with the co-ordinates of each flash counter, were provided through the courtesy of the Director, NEERI, and Mr. H. Kröninger, Lightning Research Division, NEERI.

The position of each flash counter was located on Acocks' (1975) "Veld Types of South Africa" map (scale = 1:1 500 000) to the nearest minute so that the veld type at each installation could be determined. Flash counters located on the boundary between two adjacent veld types were assigned to both types. An average annual ground-strike density for the period July 1975 - June 1981 was calculated for each veld type containing one or more flash counters by computing the average value of the mean annual ground-strike densities for all counters in that veld type. For example, three flash counters in the False Thornveld of Eastern Province (Acocks' Veld Type 21) registered mean annual ground-strike densities of 2,5, 2,7 and 0,9 strikes·km $^{-2}$·annum $^{-1}$, yielding an average value of 2,0 strikes·km $^{-2}$·annum $^{-1}$ for this veld type.

4.3 Classification of South African grasslands

South African grasses and grasslands are classified according to the nutritional value of their foliage to grazing ungulates upon reaching maturity (Scott 1947, 1951, 1955, Story 1952, Tainton 1981b, West 1965). *Sweet* grasslands are dominated by grasses in which the foliage retains most of its nutritional value upon reaching maturity, and are capable of supporting domestic livestock throughout the year without supplemental feeding (Scott 1947, Story 1952, Tainton 1981b, Weinmann 1955). Sweet grasslands are associated with relatively low annual rainfall (300-650 mm annum $^{-1}$: Acocks 1975), high ambient temperatures and eutrophic soils (Acocks 1975, Mentis & Huntley in press; Story 1952, Tainton 1981b). *Sour* grasslands are dominated by grasses in which the nutritional value of the foliage to grazing ungulates undergoes a decline upon reaching maturity, so that domesticated livestock may thrive on sour grassland for only *ca* 150 - 180 days annum $^{-1}$ without supplemental feeding (Mentis & Duke 1976, Scott 1947, 1951, 1955, Story 1952, Tainton 1981b, Weinmann 1955). Sour grasslands are associated with high annual rainfall (550 - 1 950 mm annum $^{-1}$: Acocks 1975), relatively low ambient temperatures and highly leached, dystrophic soils (Acocks 1975, Mentis & Huntley, in press, Story 1952, Tainton 1981b).

Sweet and sour grasslands represent opposite extremes of a gradient on which *mixed* grasslands occupy an intermediate position. Mixed grasslands comprise both sour and sweet grasses, and maintain a higher nutritional value to grazing livestock during autumn and early winter compared to sour grassland, so that livestock may thrive on mixed grassland for *ca* 150 - 330 days annum $^{-1}$ without supplemental feeds (Mentis & Duke 1976, Scott 1947, 1951, 1955, Story 1952, Tainton 1981b). Mean annual rainfall ranges between 400 and 900 mm, and soils tend to be mesotrophic in mixed grasslands (Acocks 1975, Mentis & Huntley in press). Mixed grassland may be classified as "sweet-mixed" or "sour-mixed", depending on the relative proportions of sweet and sour grasses in the sward (Tainton 1981b).

Inland mountain grasslands are distinguished from sour, sweet and mixed grasslands by a high proportion of temperate, evergreen C_3 grasses in the sward (Acocks 1975, Mentis & Huntley in press). Inland mountain grasslands comprise sour types on dystrophic soils in the eastern portions, and sweet types on eutrophic soils in the more westerly portions. Mean annual rainfall ranges from *ca* 1 900 mm in the east, to 500 mm in the west (Acocks 1964, 1975, Mentis & Huntley in press).

The geographic distribution of each of the four main grassland sub-groups is shown in Fig. 4.2. Sweet grasslands occur on the central interior plateau between 1 200 and 1 500 m above sea level, and in the eastern Cape Province between 350 and 650 m above sea level, mainly on flat or slightly undulating topography. Sour grasslands occur mainly along the Great Escarpment (King 1963, Wellington 1955) and other major interfluves in the eastern part of the country (Fig. 4.2), on flat-to-rolling or, in the more mountainous areas, steep topography, between 300 and 2 150 m above sea level. Mixed grasslands are situated between the sour and sweet grasslands of the interior plateau, and between the sour grassland and sweet savanna and bush-dominated communities east of the Great Escarpment (Fig. 4.2), between 600 and 2 000 m above sea level, while inland mountain grasslands occur in the Lesotho highlands and outlier mountain ranges in the eastern Cape Province, above the 1 500 m contour (Acocks 1975, Mentis & Huntley in press). Boundaries between the different grassland sub-groups indicated in Fig. 4.2 are zonal, and transitions between the sub-groups conform to soil, temperature and a rainfall gradients (Mentis & Huntley in press).

South African grasslands are also classified according to their successional status (Phillips 1930, Mentis & Huntley in press, Tainton 1981b, Tainton & Mentis in press). Extensive areas of grassland in South Africa are sub-climax communities seral to forest, macchia or savanna-woodland communities, and are maintained as open grassland primarily by fire and grazing (Acocks 1975, Bayer 1955, Killick 1963, Mentis & Huntley in press, Phillips 1930, Scott 1951, Story 1952, Trollope & Booysen 1971, West 1951). The remainder of

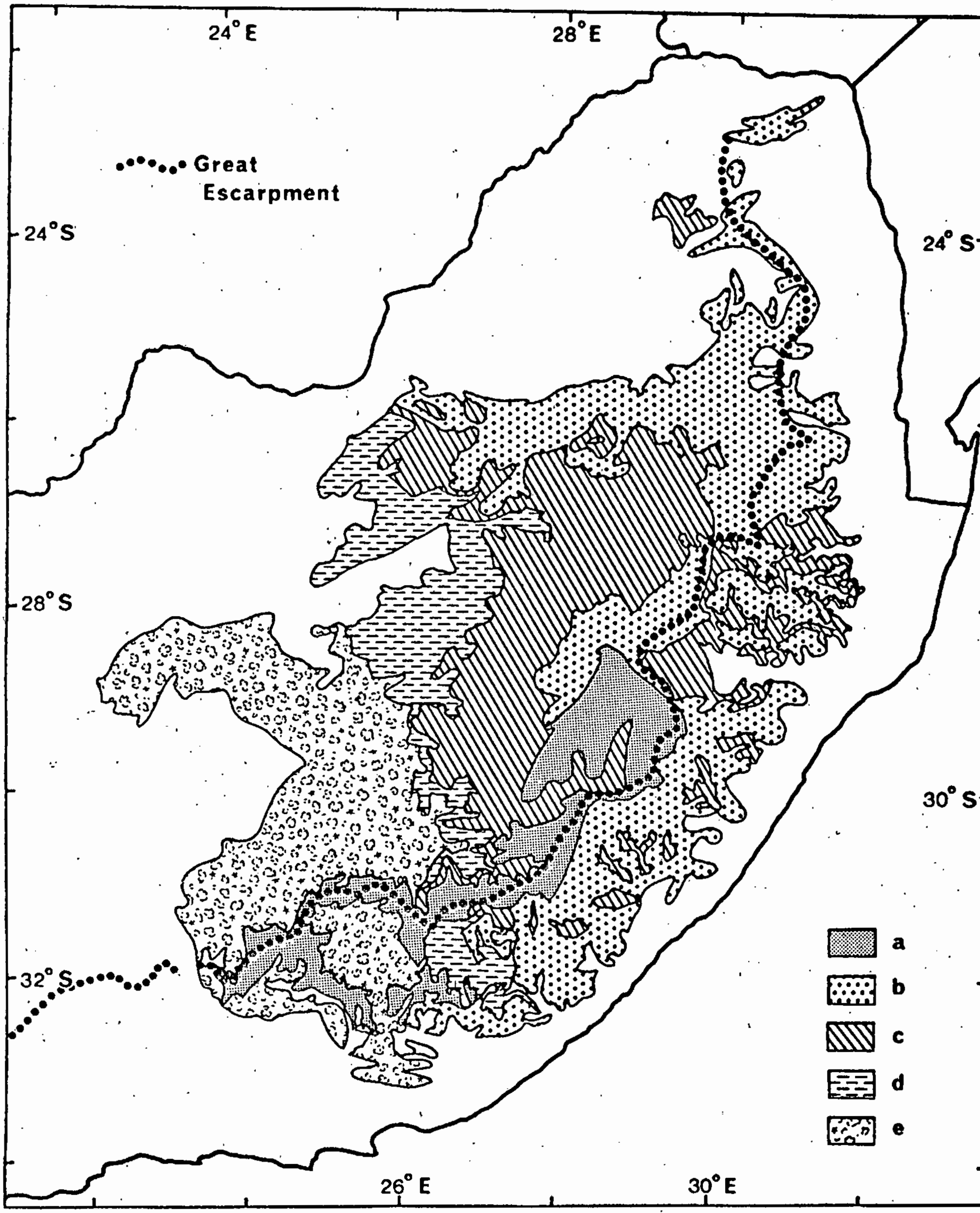

FIG. 4.2 Distribution of inland mountain grassland (a), sour grassland (b), mixed grassland (c), sweet grassland (d) and sweet grassland invaded by karoo vegetation (e), after Acocks, in Talbot & Talbot (1960).

the South African grassland biome is considered to be climax vegetation determined by climatic conditions which favour grassland but prevent the establishment of woody vegetation (Acocks 1975, Mentis & Huntley in press, Roux 1969, Tainton 1981b, Wellington 1955).

4.4 The role of fire in the South African grassland biome

4.4.1 The individual vascular plant

The aerial portions (or "topgrowth") of grasses and associated grassland herbs present ideal fuels for combustion. Grassland topgrowth is a finely divided, loosely arranged fuel type interspersed by numerous air spaces and dispersed rather homogeneously in the fuel matrix (Daubenmire 1968, Vogl 1974). Most grassland plants are surface deciduous hemicryptophytes in which the aerial parts undergo complete die-back and desiccation annually (Vogl 1974), so that fires occurring in the annual dormant phase consume mostly dead tissue (Daubenmire 1968). Because of its fine texture, grassland topgrowth is particularly sensitive to weather changes (Daubenmire 1968), so that the low relative humidities, frequent windy conditions and frosts that occur during the dormant season (late autumn and winter) in the grassland biome (Schulze 1965, Schulze & McGee 1978, Wellington 1955) hasten the desiccation of foliage, enhancing its flammability.

Grasses may produce a considerable amount of topgrowth in the course of a single growing season, especially in damp or high-rainfall areas (Kucera & Ehrenreich 1962, Rutherford 1978, Tainton 1978, Vogl 1974, West 1965). Grassland decomposition rates are usually slow, so dead plant debris accumulates more rapidly than it decomposes (Vogl 1974). Topgrowth that is not removed by burning, grazing or mowing accumulates as litter (Scott 1955), and several authors (Daubenmire 1968, Heady 1956, Kucera & Ehrenreich 1962, Tainton 1978, Vogl 1974, Weaver & Rowland 1952, West 1965) have emphasized the detrimental effects of excess litter on growth, vigour, flowering activity and seedling establishment in grassland plants. Periodic removal of accumulated litter is imperative for the survival of grassland plants, which become moribund and eventually die out in the long-term absence of canopy removal (Davidson 1964, Downing 1974, Roux 1969, Scott 1951, 1955, Staples 1926, 1930, Tainton 1978, Theron 1937, 1946, West 1965).

The deleterious effects of excess litter on grassland plants are most rapidly and acutely noticable in high rainfall areas due to more rapid rates of foliage production and litter accumulation (Kucera & Ehrenreich 1962, Scott 1951, Tainton 1978, 1981c, Vogl 1974, Weaver & Rowland 1952, West 1965) and the decreased utilization of mature foliage by grazing ungulates (Trollope 1978) in mesic grasslands. By contrast, sweet grasses, which retain high nutrition in their foliage and are utilised heavily by grazing ungulates throughout the year, may escape the need for periodic burning, except after a series of years with exceptionally high rainfall, when foliage production greatly exceeds the grazing requirements of domestic livestock (Tainton 1981c).

4.4.2 Grassland community maintenance

Burning at appropriate intervals, at the appropriate time of year, to remove excess litter promotes grassland community maintenance by maintaining the constituent plants in a healthy, vigourous condition, and by destroying seedlings of forest, macchia or savanna-woodland precursors that might invade grassland in the absence of periodic burning (Bayer 1955, Scott 1951, 1970, 1972, Story 1952, Tainton 1978, Vogl 1974, West 1965).

The most persuasive evidence of the need for periodic defoliation to maintain sour and sour-mixed grassland communities comes from experimental plots protected from fire and grazing for considerable lengths of time (Davidson 1964, Roux 1969, Scott 1951, 1972, Stapes 1926, 1930, Story 1952). The results of these experiments are all remarkably similar. After two or three years of fire/grazing-protection, the dominant perennial grasses become moribund and gradually die out, and the resultant patches of bare soil are colonised by less fire-tolerant annual grasses and weeds. When the duration of the fire/grazing-protection period is sufficiently prolonged, small shrubs may eventually become established in the plots (Davidson 1964, Roux 1969, Scott 1951, Story 1952).

Unfortunately, long-term fire/grazing-protection experiments of the type described above have all been conducted in sour or sour-mixed grassland areas where annual rainfall and foliage production are relatively high, except for an 18-year experiment in sweet-mixed grassland near Potchefstroom (mean annual rainfall = *ca* 600 mm) described by Theron (1937, 1946). After three years of fire/grazing-protection the deleterious effects of non-defoliation were apparent in the sward, as palatable grasses were suppressed and gradually died out under the mat of partially decomposed litter, to be replaced by tough, unpalatable grasses. By the 18th year of the experiment the plot was virtually unfit for grazing, and burning was advanced as the only means of effecting an improvement (Theron 1946).

Periodic burning also helps maintain open grassland communities by destroying juvenile trees and shrubs that might otherwise become established in the grassland and alter its composition (Tainton 1978, 1981c, West 1965). Around the periphery of the grassland biome there is a marked tendency for less fire tolerant vegetation from adjacent fynbos, karoo, forest and savanna-woodland communities to invade the grassland. Extensive areas of grassland in South Africa have been replaced by these peripheral communities within recent historical time, and the artificial control or elimination of fire is often advanced as an important factor in the invasion of open grassland by trees and shrubs (Acocks 1964, 1975, Edwards 1967, Galpin 1926, Phillips 1930, Scott 1951, Story 1952, Trollope 1978, Trollope & Booysen 1971). Repeated burning has proved effective in destroying the younger juvenile stages of macchia flora and *Acacia* spp. in encroached grassland, particularly in high-rainfall areas where grass fuel is produced at a sufficiently high rate to provide for frequent burning (Downing *et al.* 1978, Scott 1951, Story 1952, Trollope 1972, 1973, 1978, Trollope & Booysen 1971). By contrast, fuel production in low-rainfall areas may be inadequate to allow burning at sufficiently frequent intervals to prevent the establishment of tree and shrub seedlings, and browsing by ungulates, in combination with infrequent burning, may discourage bush encroachment in these xeric grassland areas (Trollope 1974, 1980).

Encroachment of grassland by trees and shrubs often occurs as a result of deterioration of the sward through farming malpractices, especially continuous selective grazing, over-grazing and trampling by domestic livestock, and the control or elimination of fires (Acocks 1964, 1975, Du Toit 1972, Edwards 1967, Galpin 1926, Phillips 1930, Scott 1951, Story 1952, Trollope 1972, Trollope & Booysen 1971, West 1965). Woody plants do not establish themselves readily in a healthy, vigorous sward (Du Toit 1972, Story 1952). Thus, burning at the appropriate frequency and time of year to remove excess litter and to maintain a healthy sward is of obvious importance in preventing tree and shrub encroachment.

4.5 Lightning potential over South Africa

4.5.1 Lightning ground-strike density, topography and air circulation

The annual incidence of lightning varies considerably across

South Africa (Fig. 4.3). Fig. 4.3 is based on average lightning ground-strike densities computed for each 30-minute square containing one or more lightning flash counters during July 1975 - June 1981. Mean annual ground-strike densities range from < 0,5 strikes·km $^{-2}$·annum $^{-1}$ in the western Cape Province, to > 16,0 strikes·km $^{-2}$· annum $^{-1}$ in Natal and the eastern Transvaal. Analysis of lightning ground-strike data gathered during five consecutive July-June "lightning-years" indicates high constancy in the regional distribution of lightning over South Africa from year-to-year, i.e. lightning tends to occur annually with similar intensity over the same broad geographic areas (Kröninger 1981). Moreover, the pattern of mean annual lightning ground-strike density over South Africa (Fig. 4.3) is similar to the distribution of thunderstorm days per annum over the Republic (Schulze 1965).

Topography exerts a major influence on the regional occurrence of thunderstorms over South Africa (Jackson 1947, Preston-Whyte 1971, Tyson *et al.* 1976, Wellington 1955). The eastern part of the country is dominated by highlands rising over 1 220 m above sea level (Fig. 4.4) and referred to as the "highveld" region by Wellington (1946, 1955). The Great Escarpment demarcates the interior plateau from the marginal regions (King 1963, Wellington 1946, 1955) (Fig. 4.4). The Great Escarpment is not a uniform or well-defined feature throughout its full expression, but comprises numerous separate mountain ranges, minor escarpments and spurs, and discontinuities occur where the escarpment is indistinct or non-existent (Wellington 1946, 1955).

In South Africa the Great Escarpment achieves it maximum height and abruptness in the Southern (or Natal) Drakensberg range along the Natal-Lesotho border, and along the Northern Drakensberg range in the eastern Transvaal. The Southern Drakensberg range represents the eastern and southern edges of the basaltic Lesotho massif, and is continuous for over 480 km from Xalanga Peak to Mont Aux

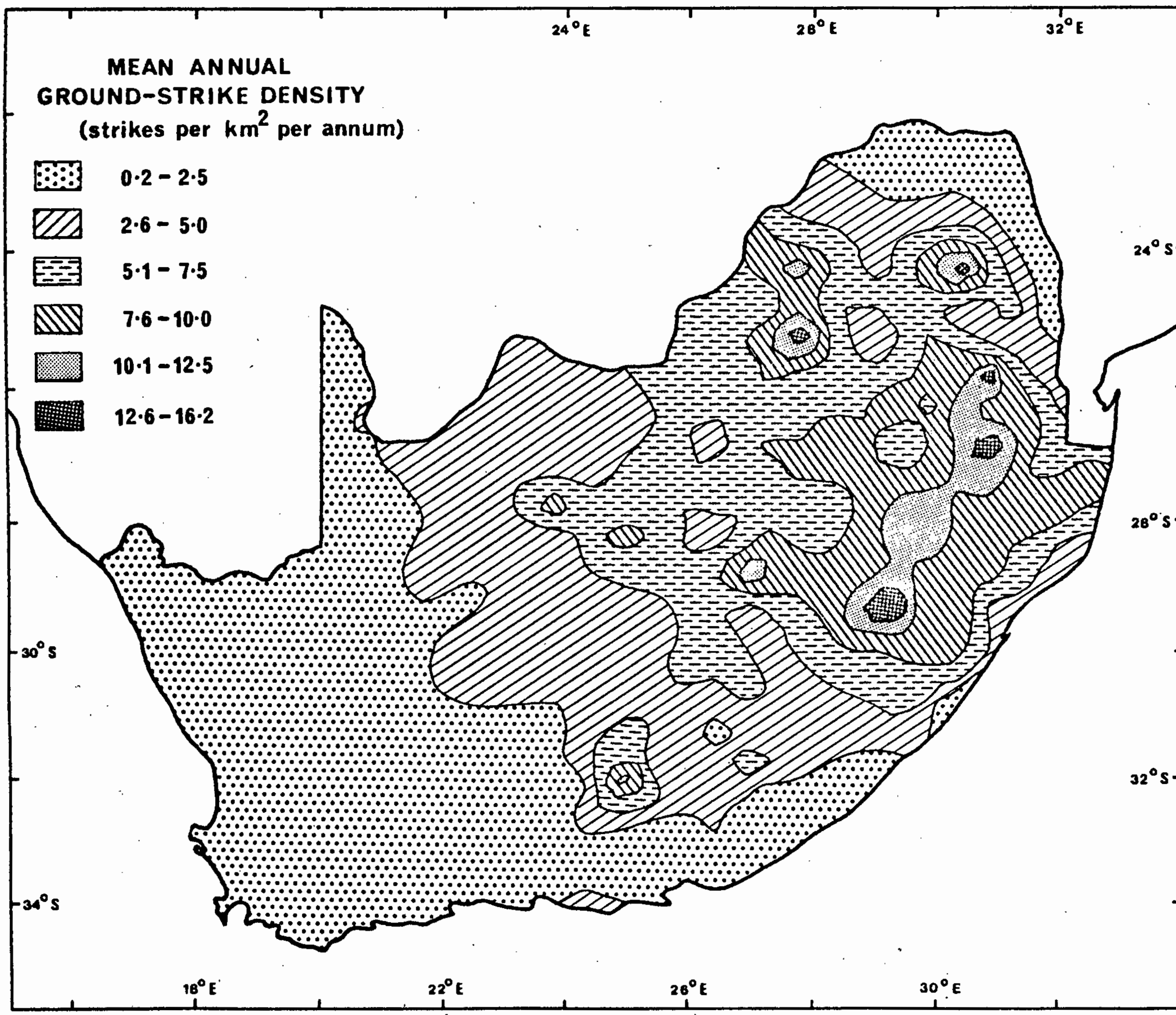

FIG. 4.3 Regional distribution of mean annual lightning ground-strike densities over South Africa, from 353 lightning flash counters operative during July 1975-June 1981 (see Fig. 4.1).

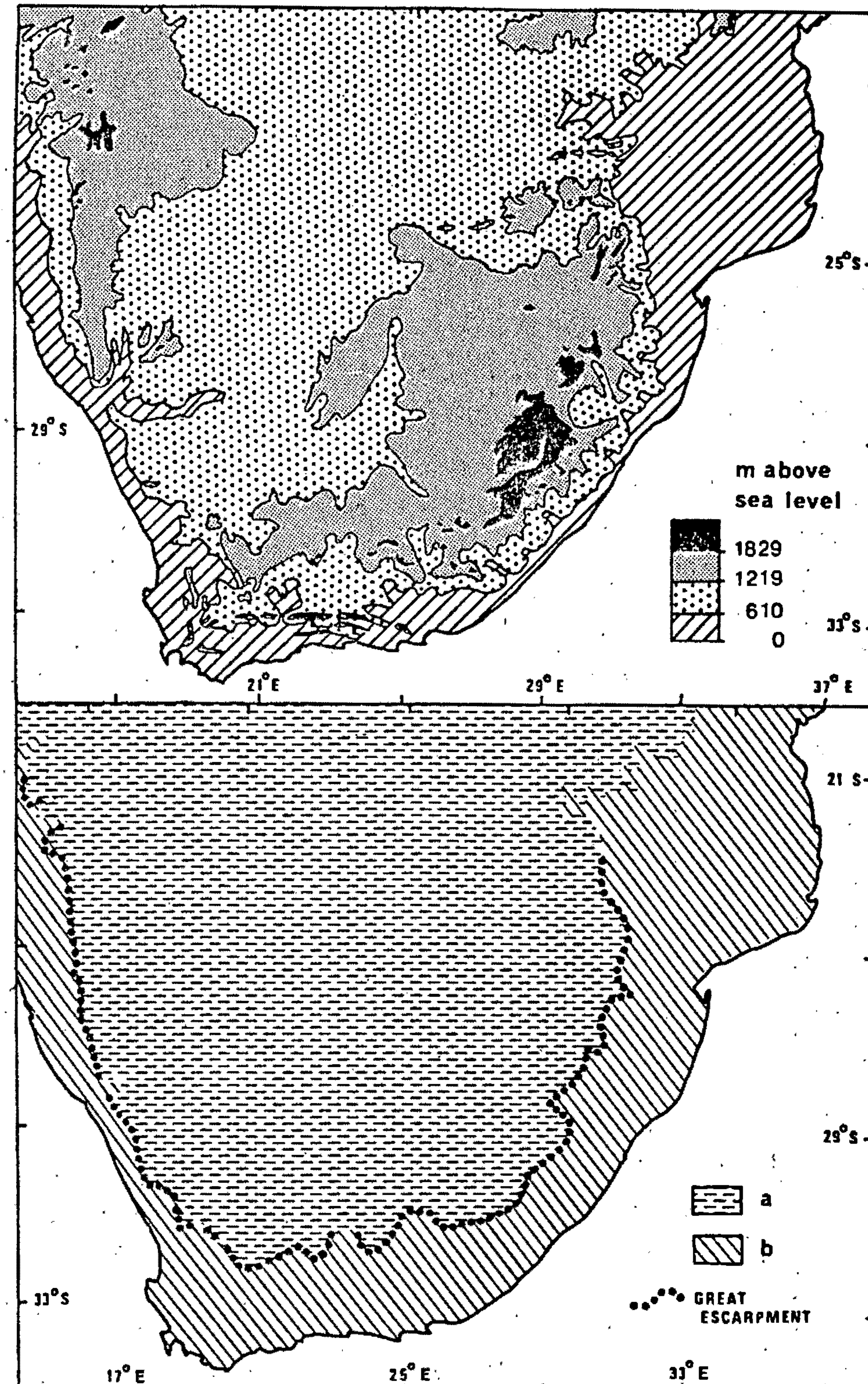

FIG. 4.4 (above) Altitudinal zones of southern Africa.

FIG. 4.4 (below) The interior plateau (a) and marginal regions (b) of the southern African sub-continent in relation to the Great Escarpment (after Wellington 1946).

Sources. In many places the Southern Drakensberg achieves heights of 3 200 m above sea level, while its foot-to-crest height ranges between 762 and 2 134 m (Wellington 1955, Killick 1963). The Northern Drakensberg is considerably lower and less abrupt than the Southern 'Berg, achieving a maximum altitude of *ca* 2 287 m above sea level, and a maximum foot-to-crest height of *ca* 915 m (Wellington 1955).

Between the Northern and Southern Drakensberg ranges the Great Escarpment is carried along the Low Drakensberg, forming the boundary between Natal and the Orange Free State at altitudes between 1 950 and 2 150 m above sea level (Wellington 1955). The northern boundary of the eastern highveld region is approximated by a ridge striking westwards from the eastern Transvaal to the Kalahari, which serves as the watershed separating the Limpopo and Orange River drainages (King 1963). The vegetation on this watershed is mainly Bankenveld (Acocks Veld Type 68), which Acocks (1975) records between 1 350 and 1 750 m above sea level.

Fig. 4.5 shows resultant surface wind directions over southern Africa during December-February (i.e. the main lightning season in South Africa). In the mornings the prevailing surface wind directions over the eastern plateau region are northerly and north-easterly, whereas those over the eastern marginal region are easterly and south-easterly. By mid-afternoon, the prevailing surface wind direction over these regions changes to north-westerly over the eastern interior plateau, and to north-easterly, easterly and south-easterly over the eastern coastal region (Fig. 4.5).

Fig. 4.5 illustrates three points pertinent to understanding the distribution of thunderstorm and lightning activity over South Africa. First, the Great Escarpment is an important climatic and meterological boundary in South Africa, effecting a partial separation of the air circulations over the interior plateau and marginal regions. Secondly, the discontinuity between the air

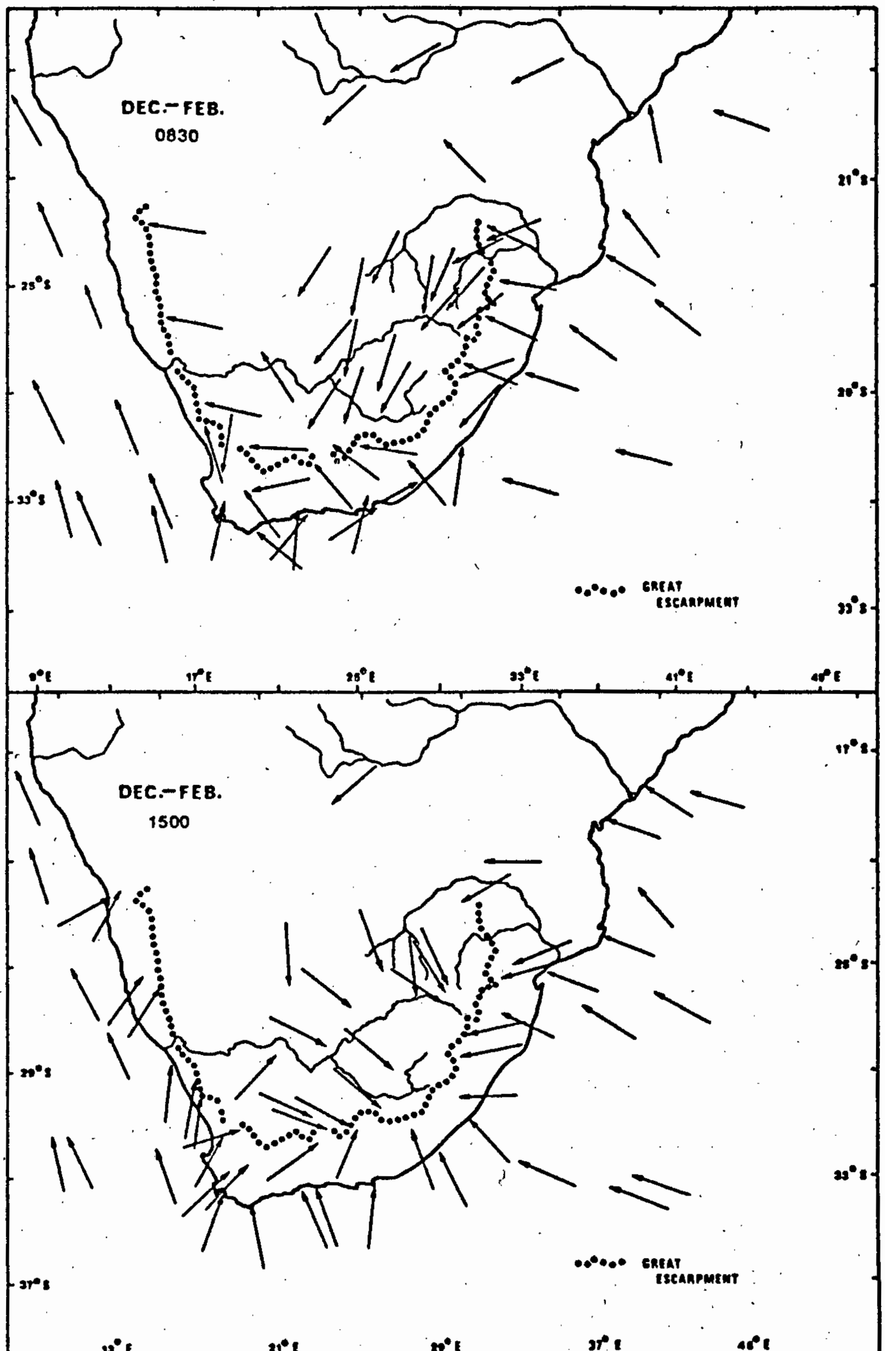

FIG. 4.5 Resultant surface wind directions over South Africa during summer, after Jackson (1947) and Wellington (1946).

circulations over the interior plateau and marginal regions are less noticable north of the highveld. Surface winds over the eastern marginal region conform to the winds in the moist, free air over the adjacent Indian Ocean, which penetrate the subcontinent far inland over the northern Transvaal and Zimbabwe via the Limpopo River and its tributaries. Thirdly, the prevailing summer surface wind directions over the eastern interior plateau and marginal regions during afternoon (i.e. when most thundersorms occur) are towards the Great Escarpment (Jackson 1947, Wellington 1946, 1955).

Thunderstorms result from interactions between discontinuous air masses possessing different moisture and thermal properties (Komarek 1968, 1972). The discontinuity between the air circulations over the interior plateau and marginal regions of South Africa, and the orientation of the prevailing surface wind directions with respect to the Great Escarpment, afford ideal conditions for the formation of thunderstorms over the eastern highveld region in summer. The highest ground-strike densities ($\geq 9{,}0$ strikes$\cdot$km$^{-2}\cdot$ annum^{-1}) are concentrated mostly along the Southern, Low and Northern Drakensberg sections of the Great Escarpment (Fig. 4.3).

Convectional storms are a common summer phenomenon over the eastern highveld (Wellington 1955), while the high incidence of thunderstorm and lightning activity along the eastern escarpment indicates the influence of slope convection on thunderstorm formation (see Tyson *et al.* 1976). Orographically-induced thunderstorms occur when moist maritime air from the Indian Ocean is forced to ascend westwards over the Southern, Low or Northern Drakensberg ranges, or southwards over the Waterberg and the Limpopo-Orange River divide in the Transvaal (Jackson 1947, Tyson *et al.* 1976, Wellington 1955). The latter movement may partially account for the high lightning ground-strike densities observed in the west-central Transvaal (Fig. 4.3)

Orographically-induced thunderstorms formed over the Southern Drakensberg range in Natal are extremely localised along the escarpment, but may occasionally travel short distances over the adjacent foothills (Tyson et al. 1976). By contrast, instability line thunderstorms formed over the Natal interior during mid-afternoon are highly mobile, sometimes travelling as far as 160 km from their site of origin before reaching the coast in the evening (Preston-Whyte 1971). Most instability line thunderstorms in Natal dissipate before they reach the coast (Preston-Whyte 1971), which may partially account for the gradual reduction of lighting activity from the escarpment to the coast (Fig. 4.3).

4.5.2 Lighting ground-strike densities in South African vegetation

Out of a total of 353 lightning flash counters installed in South Africa and Lesotho since 1975, 22 were situated on the boundary between two adjacent vegetational divisions, yielding a total of 375 records of mean annual lightning ground-strike density in 63 different veld types (Table 4.1). Mean annual lightning ground-strike densities averaged highest in inland mountain, sour and mixed grassland, whereas the lowest values were recorded in fynbos and karoo veld types (Table 4.1). The average and maximum values for mean annual lightning ground-strike density in sweet grassland veld types were inter-

TABLE 4.1 : Range and mean values of mean annual lightning ground-strike density in nine different classes of vegetation in South Africa, and the number of flash counters, and veld types containing at least one flash counter in each group or sub-group.

Vegetation group or sub-group	Total Number of Flash Counters	Total Number of Veld Types	Lightning ground-strike density (strikes·km^{-2}· annum^{-1}) Mean[a] ± S.D.	Lightning ground-strike density (strikes·km^{-2}· annum^{-1}) range
Fynbos	31	5	0,74 ± 0,81	0,2 - 3,4
Karoo	49	15	1,65 ± 1,52	0,2 - 7,2
Forest	21	3	3,07 ± 2,02	0,8 - 9,2
Savanna				
Arid	49	10	3,97 ± 2,78	0,4 - 10,4
Moist	52	6	5,62 ± 2,99	0,8 - 13,9
Grassland				
Sweet	43	4	5,01 ± 1,90	1,7 - 11,2
Mixed	41	6	6,68 ± 2,20	1,9 - 12,0
Sour	85	11	7,28 ± 2,50	1,7 - 16,1
Inland mountain	4	3	10,58 ± 4,13	6,3 - 16,2

[a]Note: Means differ significantly (one-way analysis of variance, $F = 45{,}082$, df = 374, $P < 0{,}001$).

TABLE 4.2: Significance levels of pair-wise comparisons of mean annual lightning ground-strike densities computed for each of the nine different vegetational divisions, using Scheffe's procedure of multiple comparison of means. Asterisks indicate significance at the 5% level, while NS indicates no significance.

Vegetational division[a]	Vegetational division[a] 1	2	3	4	5	6	7	8
2	NS							
3	*	NS						
4	*	*	NS					
5	*	*	NS	NS				
6	*	*	*	*	NS			
7	*	*	*	*	*	NS		
8	*	*	*	*	*	*	NS	
9	*	*	*	*	*	*	*	NS

[a]Note: Vegetational divisions are designated (1) fynbos, (2) karoo, (3) forest, (4) arid savanna, (5) sweet grassland, (6) moist savanna, (7) mixed grassland, (8) sour grassland, and (9) inland mountain grassland.

mediate between those computed for arid and moist savanna (Table 4.1).

Out of a total of 36 possible pair-wise comparisons of mean annual lightning ground-strike densities among the nine different vegetational divisions, all were statistically different except for nine comparisons (Table 4.2). A significant difference was not detected between the mean annual lightning ground-strike densities obtained in fynbos and karoo, or karoo and forest, although mean annual lightning ground-strike densities differed significantly between fynbos and forest (Table 4.2). The mean annual lightning ground-strike densities obtained in arid and moist savanna differed significantly, but did not differ significantly from that obtained in sweet grassland (Table 4.2). Sweet grassland differed significantly from mixed grassland, but neither differed significantly from moist savanna, and sour grassland did not differ significantly from mixed or inland mountain grassland, with respect to mean annual lightning ground-strike density (Table 4.2).

Average values of mean annual lightning ground-strike density computed for "pure" and sub-climax grassland veld types (as classified by Mentis & Huntley 1982) are shown in Table 4.3. The range of values recorded in each of the three groups is similar, and the mean values did not differ significantly from one another between groups (Table 4.3).

TABLE 4.3 Range and mean values of mean annual lightning ground-strike density in "pure" and sub-climax grassland sub-groups (as classified by Mentis & Huntley in press), and the number of flash counters and veld types containing at least one flash counter in each sub-group.

Grassland sub-group	Total Number of		Lightning ground-strike density ($strikes \cdot km^{-2} \cdot annum^{-1}$)	
	Flash Counters	Veld Types	Mean[a] ± S.D.	range
"Pure" grass-land	72	13	6,77 ± 2,44	1,9 - 16,2
Grassland seral to:				
Savanna	54	7	7,18 ± 2,66	0,9 - 16,1
Forest	28	4	6,59 ± 2,70	1,7 - 14,0

[a]Note: Means do not differ significantly (one-way analysis of variance, df = 153, F = 0,618; P > 0.5).

4.6 Discussion

4.6.1 The successional status of South African grasslands

Fire/grazing protection experiments indicate that at least portions of the South African grassland biome are not true climax communities in equilibrium with the climate, but are sub-climax communities seral to fynbos, heath, forest and savanna-woodland climax vegetation (Davidson 1964, Killick 1963, Mentis & Huntley in press, Roux 1969, Scott 1951, 1970, 1972, Staples 1926, 1930, Story 1952, Tainton 1978, 1981b, Tainton & Mentis in press). In the long-term absence of defoliation by fire or some other means of canopy removal, sub-climax grasslands become moribund and begin to develop towards the local potential climax vegetation (Davidson 1964, Mentis & Huntley in press, Scott 1952, 1970, Story 1952, Tainton 1978, 1981b, Tainton & Mentis in press). By contrast, the position of fire in the ecology of true climatic climax grasslands is controversial (Vogl 1974), although by implication, these grassland communities should remain stable in the absence of burning (see Tansley 1935).

South African grasslands are classified as "pure" or "true" climax types, considered to be in equilibrium with local prevailing climatic conditions, and "false" sub-climax grasslands maintained primarily by periodic burning and, to a certain extent, grazing (Acocks 1975, Bayer 1955, Mentis & Huntley in press, Tainton 1981b, Tainton & Mentis in press). In the traditional view, low ambient temperatures and frosts, seasonal moisture deficits and frequent strong winds are considered to be the main climatic features limiting the development of woody vegetation in natural grassland areas (Acocks 1975, Story 1952, Wellington 1955). By contrast, climatic conditions in the false grassland areas are considered to be amenable to the development of extensive woody vegetation, which is limited primarily by periodic burning (Acocks 1975, Edwards 1967, Mentis & Huntley in press, Tainton 1981b, Tainton & Mentis in press, Wellington 1955).

Mentis & Huntley (in press) have questioned the successional status of the so-called climatic climax grasslands in South Africa. These authors cite the Holdridge Life Zone classification of bioclimatic regions in South Africa derived by Schulze & McGee (1978), which indicates the potential for the development of extensive woody vegetation throughout the entire South African grassland biome. Moreover, fire/grazing protection experiments conducted in grasslands traditionally viewed as being climatic climax communities show that in the absence of burning or an equally effective means of defoliation, the dominant perennial grasses become moribund and die out, and are replaced by more fire-resistant grasses and weeds (Davidson 1964, Roux 1969, Theron 1937, 1946). Mentis & Huntley (in press) conclude that throughout the South African grassland biome, grassland is a sub-climax community maintained by periodic burning and grazing, and that the biome contains no "true" climax grassland. In this connection, it is interesting to note that mean annual lightning ground-strike densities average slightly higher in the so-called "pure", climatic climax grasslands, compared to those obtained in sub-climax grasslands seral to forest, and average only slightly lower than those obtained in grasslands seral to savanna. This would seem to indicate a similar potential for lightning-ignition in all three sub-groups, so that fire may have been more significant in the maintenance of so-called climatic climax grasslands than formerly recognised. The former importance of fire in the ecology of these grasslands may be obscured under present farming conditions, when domestic livestock is maintained at high densities in fenced encampments, and the sward is grazed continuously throughout the year, so that burning to remove un-utilised foliage is rarely necessary (Tainton 1981c).

The extent to which sub-climax grassland can develop towards the local climax vegetation in the absence of periodic defoliation may be limited by local factors, such as soil composition and the availability of viable seed (Davidson 1964, Killick 1963, Mentis & Huntley in press). Thus, the vegetation may be prevented from developing fully to the local climatic climax, so that in the absence of defoliation, grassland may develop to a climax stage (*sensu* Tansley 1935) more advanced than grassland, but subordinate to the local climatic climax. Moreover, localised aggregations of indigenous trees and shrubs, and patches of forest and scrub forest situated in sheltered sites that are normally protected from fires (e.g. along water courses, on steep slopes, escarpments and screes, and amongst boulder outcrops) are prevalent in grassland areas, and are sometimes interpreted as representing the local climax vegetation, which is restricted to sheltered sites because of recurrent fires (e.g. Edwards 1967, Killick 1963, West 1965). However, these sheltered sites manifest certain distinct microhabitat features that are distinctly favourable to the development of woody vegetation (e.g. enhanced moisture and protection from frosts and browsing animals), and in some instances the woody plant communities that they harbour may actually represent post-climax vegetation (Story 1952).

4.6.2 Fire and lightning in the maintenance, origin and distribution of the South African grassland biome

In the absence of grazing or other means of defoliation, periodic burning is essential to the maintenance of open grasslands in South Africa. Experiments in the contended "climatic climax" grasslands of South Africa, and in grasslands considered to be fire-maintained, sub-climax communities, indicate that following a prolonged absence of defoliation by fire, grazing or mowing, the accumulation of undecomposed litter becomes excessive, and the dominant perennial grasses begin to die out, to be replaced by less fire-resistant grasses, weeds and shrubs (Davidson 1964, Roux 1969, Scott 1951, 1972, Staples 1926, 1930, Story 1952, Theron 1937, 1946). It seems unlikely that prior to the introduction of domesticated livestock in South Africa, perhaps as early as 3 000 years ago (Hall in press), grazing by free-ranging ungulates alone would have been sufficiently reliable and uniform in time and space to ensure that most of the grassland area was defoliated at sufficiently frequent intervals to maintain a healthy, vigourous sward (Bayer 1955). Occasional burning would have been necessary to remove excess litter. This applies especially to sour and sour-mixed grasslands in high-rainfall areas, in which the rate of foliage production is particularly high, and the foliage becomes relatively unpalatable to grazing ungulates upon reaching maturity (Daubenmire 1968, West 1965).

The origins of the South African grassland biome, and its relationships with other phytochoria are obscure (Bews 1922). Conceivably, open grasslands in South Africa may have originated from pre-existing woody plant communities (e.g. fynbos, heath, savanna-woodland, forest and scrub-forest) as a result of an increase in burning frequency and intensity. Burning is effective in eradicating secondary fynbos vegetation from encroached sour grassland, and periodic burning prevents re-encroachment of restored grassland by fynbos seedlings (Downing *et al.* 1978, Trollope 1972, 1973, Trollope & Booysen 1971). In more xeric grassland and woodland areas, burning is effective in destroying or retarding the development of juvenile *Acacia* spp. and other trees (Downing 1974, Du Toit 1972, Galpin 1926, Scott 1951, Story 1952, Trollope 1974, 1980, West 1965). Burning also retards the development of established, mature trees, and reduces their capacity to reproduce (Donaldson 1966, Du Toit 1972, Trollope 1980), but is less effective in eradicating mature trees, due partly to their resistance to fire-injury, and the ability of some species to sprout from underground root stocks following a complete top kill by burning, as well as the reduction in the amount of grass fuel present (and hence cooler, less damaging fires) due to the effects of tree competition against grass for light and moisture (Du Toit 1972, Donaldson 1966, Trollope 1976, West 1965). However, periodic burning, in combination with browsing by ungulates, may prove effective in eradicating mature trees from encroached grassland (Trollope 1976, 1980).

Several types of grassland and savanna-woodland communities in South Africa possess grassy herbaceous field layers that are strikingly similar in species composition, so that the woodland is distinguished from its grassland counterpart mainly by the presence of a prominent tree component (Acocks 1975, Edwards 1967, Werger & Coetzee 1978). It is reasonable to speculate that a change in fuel production and/or ignition frequency which resulted in more frequent and destructive fires might result in the reduction or elimination of the tree component in woodland communities, resulting in open grassland. Several authors have commented on the negative relationship between burning frequency and intensity, and the height and density of trees (Kennan 1972, Killick 1963, Komarek 1976, Olindo 1972, Vogl 1974). When burning frequency and intensity exceed a certain threshold, trees may be eliminated altogether.

The time of origin and the absolute age of the South African grassland biome have yet to be determined. Palynological evidence indicates that open grassland occupied parts of the interior plateau during the late Pleistocene (Van Zinderen Bakker 1964), and Endrödy-Younga (1978) speculates that the abundance and diversity of endemic species of Coleoptera in the region, as compared to the paucity of endemic genera, indicates a relatively recent origin during the climatic fluctuations of the Pleistocene. The antiquity of the grassland biome is further evidenced by the diversity and distinctness of its endemic mammalian and avian species (Meester 1965, Winterbottom 1974).

It is reasonable to speculate that open grasslands in South Africa developed from pre-existing wooded plant communities as a result of increased burning by man. A similar hypothesis has been advanced as a possible explanation for the origin of the vast central grasslands of North America (Sauer 1950, 1956, Stewart 1956). Man has occupied southern Africa for more than 1,5 million years and may have utilised fire as early as 196,000 years ago (Frost in press, Hall in press). Throughout this extended period of human fire-utilisation, fires propagated by man have undoutedly affected the composition and distribution of grasslands and other vegetation types in South Africa (Phillips 1930, West 1965), and may have acted as a selective force in the evolution of their consituent plant and animal species. However, it can be argued that human fire-utilisation has not been prevalent for a sufficient period of time to account for the apparent antiquity of the South African grassland biome, with its rich assemblage of endemic fauna and flora, and that the origin of the grassland biome pre-dates man's use of fire in vegetation in South Africa.

As an alternative hypothesis to the above-postulated anthropopyric origin of the South African grassland biome, fires started by lightning may have been initially responsible for the origin, maintenance and distribution of the South African grassland biome. Lightning may ignite fires in vegetation when discharges occur prior to or without precipitation, or outside the range of localised showers (Vogl 1974). Lightning-ignited fires occur frequently in South African grasslands (Bayer 1955, Killick 1963, Mentis *et al.* 1974, Moll 1976, Nänni 1969, Scott 1970, West 1965). Staples (1926) describes a fire/grazing protection plot that was burnt out by a lightning-ignited fire.

Natural fires may have burnt for several days in the absence of rain, and spread across vast areas prior to the introduction of intentional and unintentional man-made firebreaks, such as roads, railway lines and cultivated lands, and controlled burning (Bayer 1955, Daubenmire 1968, Killick 1963, Nänni 1969). Old grass will burn at any time of year provided that it is sufficiently dry, but is most flämmable at the end of the winter dry season (i.e., during July-September), when weather conditions are particularly conducive to burning, and thunderstorm frequency is increasing (Mentis *et al.* 1974, Nänni 1969).

The grassland biome is centred over an area experiencing the highest thunderstorm and lightning intensities in South Africa. The exceptionally high frequency of thunderstorms and lightning over the eastern highveld results from interactions between the air circulations over the eastern interior plateau and adjacent marginal regions, which differ in their moisture and thermal properties and are separated partially by the Great Escarpment. Moreover, the Great Escarpment and the interior plateau attained their present elevation at the end of the Pliocene (King 1963, 1978). Thus, any attempt to reconstruct the vegetation of the eastern highveld region during the Pleistocene should take cognizance of the fact that the Great Escarpment has been a feature of this region for more than two million years, and throughout this period may have influenced local air circulations in such a way as to ensure that thunderstorms and lightning were prevalent in this area from the beginning of the Pleistocene, so that the vegetation in this region has long been adapted to frequent burning. This hypothesis assumes that the overall pattern of the climate in South Africa has remained relatively constant since the inception of the Pleistocene (Cooke 1964).

The high elevation of the eastern interior plateau and its adjacent marginal areas effects certain climatic conditions, notably severe frosts, occasional hail and strong winds, which might retard or prevent the establishment of woody vegetation over most of the eastern highveld and its adjacent marginal region (Acocks 1975, Tainton 1981b, Roux 1969, Story 1952, Wellington 1955). However, in the absence of a high, abrupt and extensive physiographical feature like the Great Escarpment, with its peculiar effects on the air circulations in this region, it seems unlikely that thunderstorms and lightning would be as prevalent in this region as they are today, in which case fewer natural fires would have been ignited in the past, so that fynbos, heath or scrub-forest, as opposed to grassland, would probably be the predominant natural vegetation in this region.

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GENERAL SUMMARY AND CONCLUSION

Bald ibises are primarily insectivorous, and forage mainly in indigenous grassland and in cultivated pastures in the present study area. Bald ibises prefer to feed in vegetation where the height of the foliage is lower than the level of their bellies. Thus, the birds feed extensively in burnt grassland and short, post-burn regrowth, grassland and pastures shortened by grazing and mowing, and in ploughed fields.

The grasslands inhabited by *G. calvus* are subject to extensive, controlled burning each year, primarily during winter and spring (June-October). During this period bald ibises are frequently observed feeding in burnt grassland and in short, post-burn regrowth. Sampling of macrofauna in winter-burnt grassland indicates a high abundance of potential prey items for bald ibises during the initial week after burning, largely in the form of fire-killed arthropods which the bald ibis consumes readily. Bald ibises are apparently capable of distinguishing recently burnt grassland from older burnt areas, as evidenced by the greater number of records of birds feeding in dormant, winter-burnt grassland during the initial week after burning, compared to older burnt areas.

The timing of reproduction of bald ibises at a single breeding colony was remarkably consistent in three consecutive years, and coincided with the annual prescribed burning period in the study area. That the birds began egg-laying in late winter (i.e., in late July or early August) is somewhat remarkable, considering the cold, dry conditions that prevail in the study area at this time of year. Reproductive effort and success of the ibises in the study colony were remarkably similar during the 1978 and 1979 breeding seasons, which were preceded by 12-month periods receiving between 140 and 150 % of the mean annual rainfall. By contrast, the 1980 breeding season followed on 11 consecutive months of sub-average rainfall, and reproductive performance was considerably lower in 1980, compared to the two previous years. The lower reproductive performance in 1980 may be attributed to the effects of prolonged drought on the ibises' food supply. Arthropods are generally less abundant in drought years, compared to years with normal or above-average rainfall. Furthermore, grass-burning was considerably less extensive in 1980, compared to the two previous years, and very little burnt grassland was available for the ibises to forage in. Thus, the birds were forced to seek food in alternative habitat types, primarily cultivated ryegrass pastures, which are extremely limited in their extent in the study area, and which may be less profitable in terms of the abundance of prey for bald ibises, compared to burnt grassland and short, post-burn regrowth.

The bald ibis is endemic to the South African grassland biome (Winterbottom 1974). Throughout the South African grassland biome, grassland is a sub-climax community seral to fynbos, heath, savanna-woodland, forest and scrub-forest vegetation, and grass dominance is maintained by periodic burning and, to a lesser extent, grazing by ungulates. In the long-term absence of burning or some other means of canopy removal, these grasslands become moribund and the dominant perennial grasses begin to die out, and are replaced by less fire-resistant grasses, weeds and shrubs representing more advanced stages in the local ecological succession. Even the so-called climatic climax grasslands of the interior plateau require periodic defoliation to maintain the sward in a vigorous, healthy condition. Prior to the advent of modern farming and continuous grazing by domestic livestock, grazing by free-ranging, migratory ungulates would have been insufficient to prevent the accumulation of excess litter, and occasional burning would have been necessary to remove un-utilised foliage.

The South African grassland biome is centred over an area experiencing the highest thunderstorm and lightning frequencies in South Africa. Although most grass fires today are started by man, there is ample evidence to suggest that prior to the advent of human fire-utilisation in southern Africa, fires ignited by lightning were responsible for the maintenance of extensive open grassland communities in this region, which are replaced by fynbos, heath, savanna-woodland, forest and scrub-forest communities where fire is controlled or eliminated (see Mentis *et al.* 1974). Thus, periodic burning has probably been a feature of this area for considerable time, perhaps from the very beginning of the Pleistocene, when the grassland biome probably originated, and the bald ibis' present relationship to grass-burning may have evolved under natural selection, rather than being a recent development in response to fires introduced by man.

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