

## The distribution and biology of nomadic birds in the Karoo, South Africa

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**Abstract.** Dryland nomadic bird species, as a proportion of all bird species in a biome in southern Africa, are highest in the arid grassland and arid and semi-arid Karoo in South Africa. Nomadic birds, of which the most widespread species is the greybacked finchlark *Eremopterix verticalis* (Smith), are most frequently observed in the north-central and north western Nama Karoo. The species richness of nomadic species is inversely correlated with species richness of all bird species in the Karoo. Since the distribution of nomadic birds is in areas where rainfall is patchy, low (<250 mm per year) and aseasonal, this supports the idea that fewer species are able to cope with resources that are patchy in time and space, and that there has been selection for nomadism in the species that are able to use patchy environments. Species richness and abundance of nomadic birds is negatively correlated with rainfall amount but positively correlated with the coefficient of variation of the rainfall and with rainfall in autumn. The frequency of nomadic birds is inversely correlated with altitude range; nomadic species are most often recorded in structurally simple habitats

(shrubland and grassland) on open plains. Most nomadic bird species in the Karoo are granivorous. Perennial desert grasses are important components of the habitat and diet of small nomadic granivores, and also provide nest sites and nest material. Nomadic birds can breed throughout the year, without a clearly defined 'season' in both the Succulent and Nama Karoo. Average clutch sizes do not differ significantly between resident and all nomadic species in the arid and semi-arid Karoo. Nomadism is an evolutionary stable strategy for individual species only when extremes in environmental conditions are frequent enough, and unpredictable enough, to maintain movements to high resource patches or to maintain dispersal away from low resource patches. If high rainfall years are too regular or infrequent, or peaks in fluctuations of resources in the environment too low, or rainfall patches are randomly distributed, nomadism would not be maintained as part of the individual behaviour pattern.

**Key words.** Granivorous birds, arid, semi-arid, Karoo, avian biogeography, larks, southern Africa.

### INTRODUCTION

Movements in animals may be either seasonal and predictable ('migration'), directional one-way movements ('emigration') (Sinclair, 1984) or undirected dispersal (Greenwood, 1984). Dispersal usually refers to one-way movements from high-resource areas, where survival and reproduction may be relatively high, and is considered to be an adaptation to avoid inbreeding and to reduce competition between relatives (Greenwood, 1984). Nomadism, in which the movements are irregular and where destinations may differ from year to year is a form of emigration (Sinclair, 1984) and is considered to be an adaptation to use resources that are patchy in space and time. Unlike dispersal, all members of a nomadic species may leave an area, and move together to another patch, so that competition between individuals is not necessarily reduced and inbreeding not necessarily avoided. Nomadic species may return to the same area to breed, or they may move to other areas, depending on environmental conditions.

The evolution of nomadism in animals is favoured by

unpredictable patchiness or clumping of resources in space and time (Sinclair, 1984). Arid and semi-arid ecosystems are characterized by low and unpredictable annual rainfall (Noy-Meir, 1973) and rainfall events are often highly localized so that patches of vegetation at different phenological stages are scattered across the landscape. Birds that are able to move quickly and efficiently to these patches may enjoy abundant food and shelter (nest sites) and a lack of intense competitive interactions, so that selection would favour local and regional movements by birds. Nomadism appears to be most prevalent among granivorous birds inhabiting arid or semi-arid ecosystems (Maclean, 1974; Davies, 1984). Such arid and semi-arid environments as the Succulent and Nama Karoo (the Karoo *sensu lato*), South Africa, tend to have only residents or nomads among the avifauna (Maclean, 1974), although some Palaearctic migrants occur regularly throughout the semi-arid Karoo. Palaearctic migrants and intra-African migrants may be 'resident' in one area for the period of their stay, or they may be nomadic, moving about the Karoo in the same way as the Karoo nomadic species. Vernon (1986) hypothesized that there should be fewer residents, and greater nomadism

and aseasonal breeding with decreasing rainfall in the Karoo.

The objectives of this paper are to identify the part of the Karoo most commonly occupied by nomadic birds and to examine the factors affecting the distribution, breeding and species richness of nomadic birds. There are two categories of nomadic birds: those that are nomadic on a regional scale (nomads), and those that are nomadic on a landscape scale (local nomads). Local nomads tend to vary in numbers of individuals present at a locality; nomads vary both in number of individuals and in species richness. Noy-Meir (1973) makes the point that the inclusion of nomads in ecosystem models requires modelling at the regional, rather than the local, scale. Although local nomads are briefly discussed, this paper is essentially concerned with those species that are nomadic on a regional scale and that use dryland habitats. Key questions are: (1) where in the Karoo are nomadic birds most common? (2) can their distribution be related to particular weather patterns? and (3) can their distribution be related to particular vegetation types?

## METHODS AND DATABASES

### Distributions of birds and source of distributional data

Distributions of birds were mapped using a Geographic Information System (GIS) program. The data on frequency of occurrence of various bird species were analysed using the same program. The GIS program used in this study is PC ARC/INFO 3.4D PLUS (Environmental Systems Research Institute, Redlands, California, U.S.A.). The vector capabilities of PC ARC/INFO can map exact boundaries of map units (see Haslett (1990) for further discussion). The topographic input data ( $15' \times 15'$  cells, approximately  $27.25 \times 23.5$  km (*c.* 640 km<sup>2</sup>) at the latitudes and longitudes at which this study was completed) was fairly coarse, but this resolution does provide broad geographic patterns of the focal species' distributions and provides a basis for more detailed studies at a finer scale.

My procedure was to computerize coded distribution data of all avifauna currently recorded from the Karoo, using codes for each  $15' \times 15'$  square ('quarter-degree square' (QDS); see Edwards & Leistner, 1971; Leistner & Morris, 1976; Harrison, 1992). The main bird database used was that compiled by the Southern African Bird Atlas Project (SABAP) (Harrison, 1989, 1992). This has been supplemented by the bird distribution database compiled by Cape Nature Conservation and my own personal field records. The data consist of lists of birds entered on field cards, with separate field cards being completed for each month and locality. The field cards provide data on presence of species only, generally without any data on abundance or relative frequency of occurrence. I calculated a 'reporting rate' (Harrison, 1989, 1992; Robertson *et al.*, 1995) that provides a 'relative abundance index' for each bird species. The reporting rate is the number of observations of the species at a locality divided by the number of field cards for the locality. This probably gives an unrealistically high

index for species in squares for which there are few cards. However, in the absence of census data, this is the only way of evaluating the occurrence of species beyond simple presence or absence. Sources of error in the database include misidentifications of birds and mis-keyed code numbers in the two major bird databases, the patchy distributions of birds as a result of poor coverage of parts of the Karoo by ornithologists.

I categorized all bird species in the Succulent and Nama Karoo as residents, nomads or local nomads on the basis of published accounts of their biology (Maclean, 1993) and my personal knowledge of their behaviour in the Karoo. These data were supplemented by my own records of food of nomadic birds (mainly stomach and crop contents) and breeding records collected over the period 1986–93 in the Karoo. Data on the food of granivorous birds were from road casualties picked up in various parts of the Karoo and from birds collected during the course of other studies (e.g. Transvaal Museum collections; Dean *et al.*, 1991). Seeds from stomachs and crops were examined under a  $40 \times$  binocular microscope and, where possible, were identified to genus using a reference collection of seeds from identified plant specimens.

The structural heterogeneity of habitats was classified using Acocks (1953). All habitats in the Succulent and Nama Karoo were placed in one of five classes, one being relatively homogeneous (sparse grassland), and five being relatively structurally heterogeneous (arid savanna woodland). The distributions of grasses were taken from Gibbs Russell *et al.* (1990), Zacharias (1990) and van Breda & Barnard (1991).

Data on the relative abundance of plant growth forms were taken from an unpublished manuscript entitled 'Veld types of the western half of the Republic of South Africa' by J. P. H. Acocks (National Botanical Institute, Kirstenbosch). This manuscript gives various plant growth forms as a percentage of all growth forms in each of Acocks' (1953) veld types.

## RESULTS AND DISCUSSION

### Biogeography and species richness of nomadic birds

Nomadic and locally nomadic species in the Karoo are given in Table 1. Several species, particularly the sunbirds, may be more sedentary in other biomes. Movements in some of the columbids are also not well known. Rock pigeon *Columba guinea* Linnaeus, turtle dove *Streptopelia capicola* (Sundevall) and laughing dove *S. senegalensis* (Linnaeus) appear to be resident in the Karoo, but there may be local movements in all three species. Table 1 does not include aquatic species, although all aquatic species in the Karoo are nomadic to some extent.

Nomadic bird species (including local nomads), as a proportion of all species in a biome in southern Africa, is highest in the arid grassland and Karoo (Fig. 1). Two species, pinkbilled lark *Spizocorys conirostris* (Sundevall) and chestnutbacked finchlark *Eremopterix leucotis* (Stanley) do not occur in the Succulent Karoo, and Slater's lark *Spizocorys sclateri* (Shelley) is rare in the Succulent Karoo,

TABLE 1. Nomadic and locally nomadic species of birds in the Karoo and their frequency of occurrence in quarter-degree squares (of 676 possible squares). Specific names for all species in the tables are given in Appendix 1.

Species	Frequency
<b>Nomadic species</b>	
Tawny eagle	10.4 ( 70)
Namaqua sandgrouse**	84.2 (569)
Burchell's sandgrouse*	4.3 ( 29)
Redcapped lark	71.2 (481)
Pinkbilled lark*	10.5 ( 71)
Slater's lark**	10.5 ( 71)
Stark's lark*	16.3 (110)
Chestnutbacked finchlark	3.7 ( 25)
Greybacked finchlark*	75.9 (513)
Blackeared finchlark**	42.8 (289)
Wattled starling	54.3 (367)
Scalyfeathered finch	30.5 (206)
Blackheaded canary**	73.5 (497)
Larklike bunting*	91.4 (618)
<b>Locally nomadic species</b>	
Blackbreasted snake eagle	18.3 (124)
Lanner falcon	41.6 (281)
Ludwig's bustard**	65.2 (441)
Burchell's courser*	17.2 (116)
Doublebanded courser	41.0 (277)
Namaqua dove	94.2 (637)
European swift	22.9 (155)
Sentinel rock thrush*	5.3 ( 36)
Anteater chat*	89.2 (603)
Yellowbellied eremomela	77.1 (521)
Fantailed cisticola	26.9 (182)
Chat flycatcher*	80.6 (545)
Fairy flycatcher**	60.5 (409)
Malachite sunbird	48.7 (329)
Lesser doublecollared sunbird*	45.6 (308)
Greater doublecollared sunbird*	6.5 ( 44)
Dusky sunbird**	68.8 (465)
Black sunbird	5.3 ( 36)
Redbilled quelea	33.0 (223)
Redheaded finch*	38.5 (260)
Blackthroated canary	39.6 (268)
Yellow canary*	92.0 (622)
Whitethroated canary*	88.5 (598)
Streakyheaded canary	14.3 ( 97)
Rock bunting	16.4 (111)

\*Southern African endemic (Clancey, 1986). \*\*Karoo endemic.

but there is otherwise no difference in species richness of nomadic birds between the Succulent Karoo and the Nama Karoo biomes.

The distribution of nomadic species, showing their occurrence relative to all species recorded in a quarter-degree square, is given in Fig. 2. Nomadic birds, of which the most widespread species is the greybacked finchlark *Eremopterix verticalis*, occur throughout the Karoo, but are most frequently observed in the north-central and north western Nama Karoo, whereas locally nomadic species appear to be more frequently observed in the eastern Nama Karoo. The reporting rate of nomadic species is inversely, and significantly, correlated ( $r^2=0.09$ ,  $y=0.17-0.005x$ ,  $P<0.001$ ) with species richness of all species in the Karoo

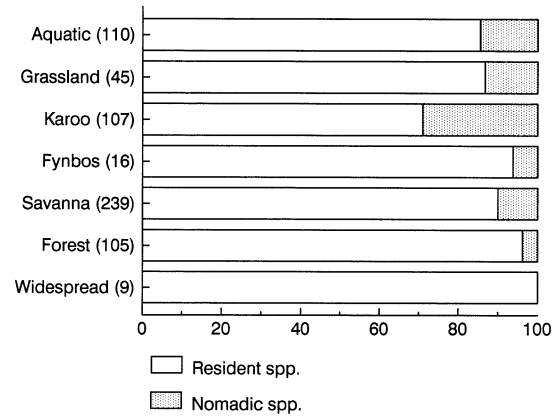


FIG. 1. The percentage of nomadic and locally nomadic species of birds in terrestrial biomes in southern Africa. The total number of non-migratory breeding species is given in parentheses after the name of the biome, and species have been placed in their most typical habitat. Numbers of species are from Maclean (1993). The Succulent Karoo and the Nama Karoo have not been separated. Marine and estuarine species have been excluded from the table.

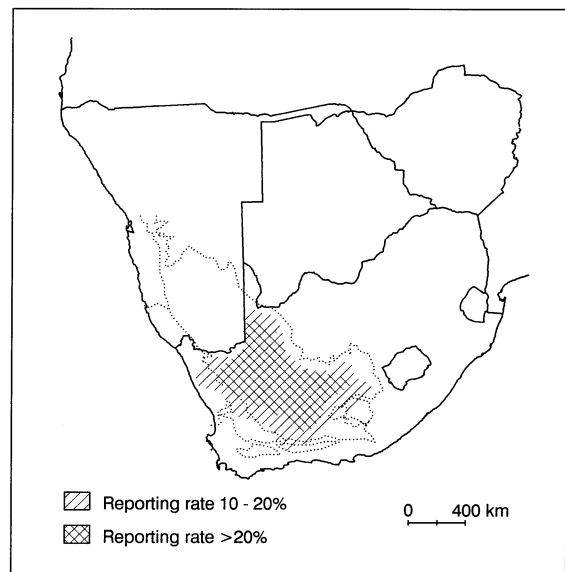


FIG. 2. Southern Africa, showing the Karoo *sensu lato* bounded by the dotted line, and the relative abundance (as indicated by the reporting rate; see text) of nomadic bird species in the Karoo.

(Fig. 3). Since the distribution of nomadic birds in the Karoo also appears to be mainly in areas where rainfall is patchy, low and aseasonal, this supports the idea that fewer species are able to cope with resources that become unpredictable in time and space, and that there has been selection for nomadism in the species that are able to use patchy environments. The distribution of nomadic birds in the Karoo appears to be mainly in areas where the mean annual precipitation is below 250 mm (Fig. 4) and is significantly and negatively correlated with rainfall amount ( $r^2=0.11$ ,  $y=0.17-0.02x$ ,  $P<0.001$ ), and the coefficient of variation of rainfall ( $r^2=0.21$ ,  $y=-0.03+0.02x$ ,  $P<0.001$ ) (Fig. 5). However, a stepwise model, with the relative

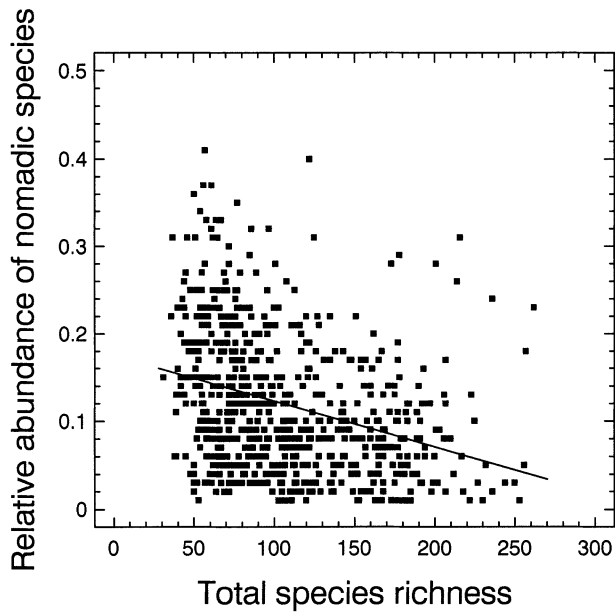


FIG. 3. A regression of the reporting rate of nomadic species in each quarter-degree square against total species richness in the Karoo *sensu lato*.

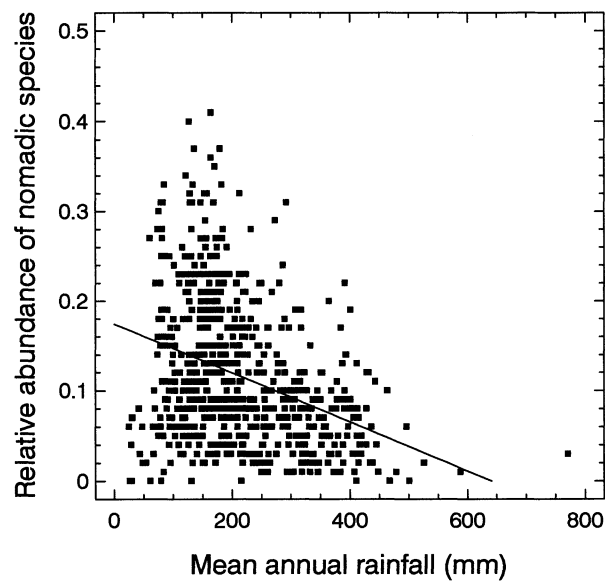


FIG. 4. A regression of the reporting rate of nomadic species in each quarter-degree square against mean annual precipitation in the Karoo *sensu lato*.

abundance of nomadic birds as the dependant variable, and mean annual precipitation, rainfall seasonality, habitat structure and proportion of succulent and annual plants, and grasses in the vegetation as independant variables, showed that the amount of autumn rainfall, habitat structure and the proportion of annual forbs in the vegetation were the most important factors influencing the distribution of nomadic birds ( $r^2=0.37$ , d.f.=576), and that rainfall amount was relatively unimportant. A matrix showing these correlations is given in Table 2.

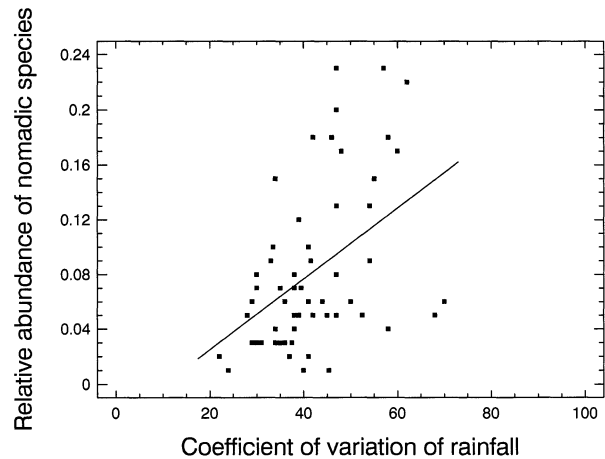


FIG. 5. A regression of the reporting rate of nomadic species against the coefficient of variation in rainfall in the Karoo *sensu lato*.

Nomadic birds occur in most habitats in the Succulent and Nama Karoo, but they are much less common on rocky slopes, inselbergs and mountains, and they tend to avoid the relic fynbos patches on mountain tops. The reporting rate of nomadic birds is inversely and significantly correlated with altitude range; nomadic species are most frequently recorded in habitats that are fairly flat, and are most common where the range in height is less than 200 m over a quarter-degree square (Fig. 6) (Succulent Karoo:  $r^2=0.18$ ,  $y=0.1-5.45x$ ,  $P<0.001$ ; Nama Karoo:  $r^2=0.2$ ,  $y=0.18-0.001x$ ,  $P<0.001$ ). These flat areas are plains shrubland and arid grassland with perennial desert grasses (*Stipagrostis brevifolia* (Nees) de Winter, *S. ciliata* (Desf.) de Winter and *S. obtusa* (Del.) de Winter), the annual grass *Schmidtia kalahariensis* Stent and annual forbs. The widespread and common desert perennial grass *S. uniplumis* (Licht.) var. *uniplumis* is often the dominant plant in nomadic bird breeding habitats in the Namib Desert, but appears to be relatively uncommon in the north western Nama Karoo. The small granivorous larks (Sclater's lark, Stark's lark *Eremalauda starki* (Shelley), greybacked finchlark, blackeared finchlark *Eremopterix australis* (Smith)) and larklike bunting *Emberiza impetuani* Smith, however, are not confined to *Stipagrostis* spp. grasslands, and in some years are abundant in other grassland and shrubland habitats. For example, in high rainfall years pinkbilled lark and greybacked finchlark may be abundant in the eastern Nama Karoo (James, 1921, 1929; Collett, 1982) in grassy patches in which *Aristida* spp., *Eragrostis* spp. and *Themeda triandra* Forssk. are common. Other desert annual grass species can provide suitable habitat at times, and both greybacked finchlarks and larklike buntings were present in large numbers in ripening *Stipa capensis* Thunb. grassland at Vanrhynsdorp in September 1994 (pers. obs).

#### Food of dryland nomadic birds

Most nomadic bird species in semi-arid regions throughout the world are granivorous (Maclean, 1974; Davies, 1984).

TABLE 2. A Spearman rank correlation matrix between the relative abundance of nomadic birds (nomads), rainfall amount, percentage autumn rainfall, structural diversity of habitats, percentage succulent plants, percentage annual forbs and percentage grasses in the vegetation.

	Nomads	Rainfall	Autumn	Habitat	Succulence	Annuals	Grasses
Nomads	1.0	-0.27	0.522	-0.337	-0.118*	0.446	0.162
Rainfall		1.0	-0.352	0.19 NS	-0.519	-0.587	0.528
Autumn			1.0	-0.143	-0.241	0.430	0.185
Habitat				1.0	0.319	-0.518	-0.256
Succulence					1.0	0.134*	-0.805
Annuals						1.0	-0.107*
Grass							1.0

\* =  $P < 0.05$ . NS = not significant.

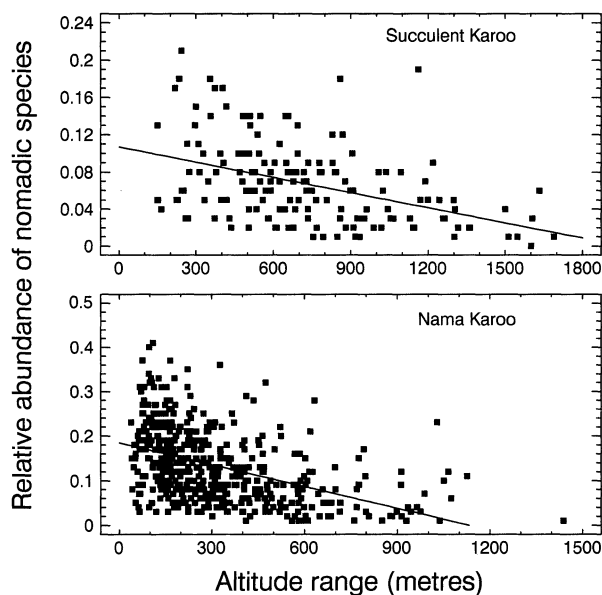


FIG. 6. A regression of the reporting rate of nomadic species against altitude range in each quarter-degree square in the Succulent and Nama Karoo.

Regional nomads in the Karoo are mainly granivorous, whereas local nomads tend to be mainly insectivorous (Table 3). There are also a number of locally nomadic species that are granivorous and nectarivorous. The relative proportion of granivory in nomads is significant (Fisher's Exact Test,  $P = 0.007$ ). Similarly, the relative proportion of insectivores among the local nomads is significant (Fisher's Exact Test,  $P = 0.007$ ).

A discriminant function analysis of the food of all ground-foraging birds for which I have detailed stomach contents analyses shows that there is some overlap in the food of residents, local nomads and nomads (Fig. 7a). The food data were log transformed for the analyses. Both discriminant functions are significant, although the status is well defined by the first discriminant function alone (relative percentage 84.7%, Wilks-Lambda = 0.522, chi-square = 118.96,  $P < 0.001$ ). To remove the possible influence of phylogenetic position on these results, a discriminant function analysis using data only for larks (Alaudidae) was done. There are no locally nomadic larks, so the species were grouped into savanna species, Karoo shrubland species and arid grassland species.

The arid grassland species are all nomads. The plot is shown in Fig. 7b. Both discriminant functions are significant (relative percentage 87.4, Wilks-Lambda = 0.441, chi-square = 116.57,  $P < 0.001$ ), so differences in diet are fairly well defined. The arid grassland species show very little overlap in diet with the shrubland species, whereas the savanna species overlap considerably in diet with both grassland and shrubland species. The results of both tests, in general, suggest that arid grassland larks differ from shrubland larks in their diet, and that there is a similar difference between nomads and residents. From this I infer that nomads differ markedly in diet from residents.

There is some difference in the kinds of seeds that are eaten by resident, nomadic and locally nomadic avian granivores in the Karoo. Summarized data on the seed components of the food of twenty-five resident, nomadic and locally nomadic species from the Karoo are presented in Table 4. Resident species feed on the seeds of forbs, shrubs and legumes. The small nomadic larks and buntings feed mainly on the seeds of perennial and annual grasses (*Brachyaria glomerata* (Hack.) A. Camus, *Centropodia glauca* (Nees) T.A. Cope, *Stipagrostis* spp. and *Schmidtia kalahariensis*), occasionally on the seeds of ephemeral Asteraceae and occasionally legumes, whereas the Namaqua Sandgrouse *Pterocles namaqua* (Gmelin) feeds largely on legumes (Table 4). Locally nomadic species feed mainly on the seeds of forbs and shrubs. Nomadic species eat a significantly larger proportion of grass seeds (Kruskal-Wallis test,  $P = 0.016$ ) than do locally nomadic species or residents.

Small (<25 g) species eat proportionately more grass seeds than larger birds in the Karoo (Mann-Whitney  $U$ -test:  $Z = -2.925$ ,  $P < 0.003$ ). The samples in Table 4 are too small to test differences in the proportion of legume seed eaten by resident and nomadic birds. Legumes appear to be important only for some of the resident larks and the Namaqua sandgrouse (see Maclean, 1995). Dixon & Louw (1978) found that Namaqua sandgrouse in the Namib Desert feed almost exclusively on legume and forb seeds. Lists of carefully identified seeds from stomachs and crops of many of the granivorous species in southern Africa are not available, so the conclusions drawn from the above analysis are tentative. The results also support Morton & Davies (1983), who found that small birds (<100 g) in the Australian arid zone eat proportionately more grass seeds than other

TABLE 3. Number of nomadic or locally nomadic species of birds in each of the major diet groups. Data from Maclean (1993).

Status	Aquatic	Raptor	Inverts.	Seeds	Nectar
Nomad	6	1	1	12	0
Local nomad	2	2	10	8	5

Species	Wt	<i>n</i>	Grass	Others	Legumes	Tot. seeds
<b>Local nomads</b>						
Namaqua dove	40	3	0	1	0	6843
Yellow canary	17	6	0.05	0.95	0	263
Whitethroated canary	27	7	0	1	0	242
Rock bunting	15	1	1	0	0	32
<b>Nomads</b>						
Namaqua sandgrouse	180	4	0	0.63	0.37	16067
Slater's lark	20	6	0.99	0	0.01	157
Stark's lark	19	16	0.90	0.10	0	377
Greybacked finchlark	17	30	0.99	0.01	0	869
Blackeared finchlark	15	8	0.67	0.33	0	360
Scalyfeathered finch	11	1	1	0	0	63
Blackheaded canary	12	3	0.85	0.15	0	200
Larklike bunting	15	6	0.91	0.09	0	138

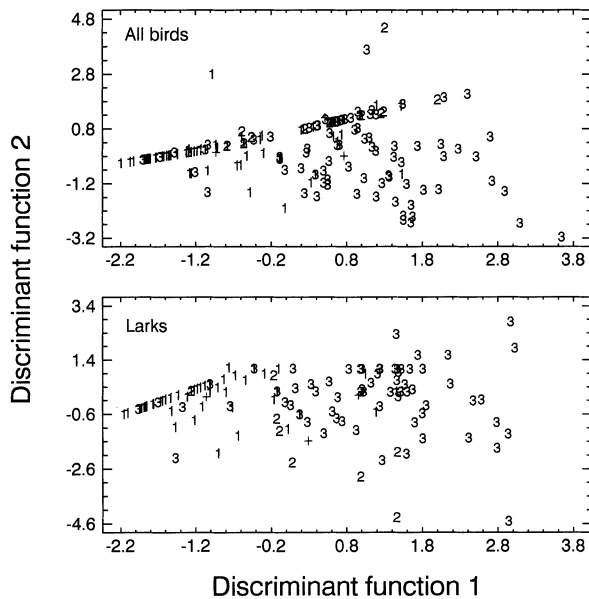


FIG. 7. (A: all birds). Plot of a discriminant function analysis of the food of nomadic species (1), locally nomadic species (2) and resident species (3). (B: larks). Plot of a discriminant function analysis of the food of larks (Alaudidae). Arid grassland species (1), savanna species (2) and shrubland species (3).

seeds. It would be of interest to test the generality of these findings in all arid ecosystems.

The advantages of eating grass seeds, particularly for nomadic birds, are that the seeds are often abundant after rain, the seeds are easily harvested and handled, and they lack the tannins and alkaloids often present in the seeds of forbs and shrubs (Watt & Breyer-Brandwijk, 1962). Seeds of grasses are produced relatively quickly after suitable rain (ca. 4 weeks from rain to seeding in *Stipagrostis ciliata*

(pers. obs). There are few data available for the Karoo on numbers of grass or shrub seeds on the soil surface. A study in progress suggests that forb and shrub seeds may be abundant (up to 6 g/m<sup>2</sup>) on sandy soils in the northern Nama Karoo (Lloyd, Little & Crowe, 1994).

#### Reproduction in nomadic birds

Rainfall and its effects apparently initiate breeding in birds in the southern African arid zone (reviewed by Maclean, 1990, 1995). Although this has been stated many times there has been very little, if any, research on the ecosystem processes involved and the length of time various processes take to ultimately provide the resources that add up to suitable breeding habitat for birds. The threshold rain amount (how much rain in how much time sets the tip over to growth and seeding of grasses and breeding by birds?) is not known for the Karoo. In the southern Kalahari, Maclean (1970c) found that >25 mm of rain is needed to initiate breeding in birds that nest opportunistically, and that breeding was initiated more rapidly after rain (i.e. a lower threshold rain amount) in summer than in winter. Although some birds may start nesting within seven days of rain (Maclean, 1995), there is likely to be a longer lag between rain and the time that granivores can begin nesting than between rain and when insectivores begin nesting.

In the north western and northern Karoo, the small nomadic granivores (pinkbilled lark, Slater's lark, Stark's lark, greybacked finchlark, blackeared finchlark and larklike bunting) line their nests with the awns of *Stipagrostis* spp. grasses (usually *S. ciliata*) (Dean *et al.*, 1992; pers. obs.). Awns of these grass species are 40–50 mm long, and are fluffy and white. The seeds are wind dispersed (Gibbs Russell *et al.*, 1990). A common occurrence in the central and northern Nama Karoo some weeks after rain has fallen is the wind-drifted heaps of *Stipagrostis* spp. awns that collect

TABLE 4. The proportion of different kinds of seeds in combined stomach and crop contents of granivorous or partly granivorous birds in the Karoo. Only the seed component of the diet of individual birds is given here. Wt = average weight of adult bird, males and females combined.

Species	Wt	<i>n</i>	Grass	Others	Legumes	Tot. seeds
<b>Residents</b>						
Fawncoloured lark	23	2	0.54	0.46	0	270
Sabota lark	25	9	0.69	0.27	0.04	99
Longbilled lark	50	3	0	1	0	15
Karoo lark	31	33	0.13	0.77	0.10	3501
Red lark	37	12	0.27	0.73	0	832
Spikeheeled lark	27	8	0	0.97	0.03	252
Redcapped lark	26	2	0.02	0.98	0	64
Thickbilled lark	44	4	0.04	0.93	0.03	295
Cape sparrow	27	1	0	1	0	5
Masked weaver	26	1	0	1	0	29
Cape canary	15	2	0	1	0	40
Cape bunting	21	1	0	1	0	53

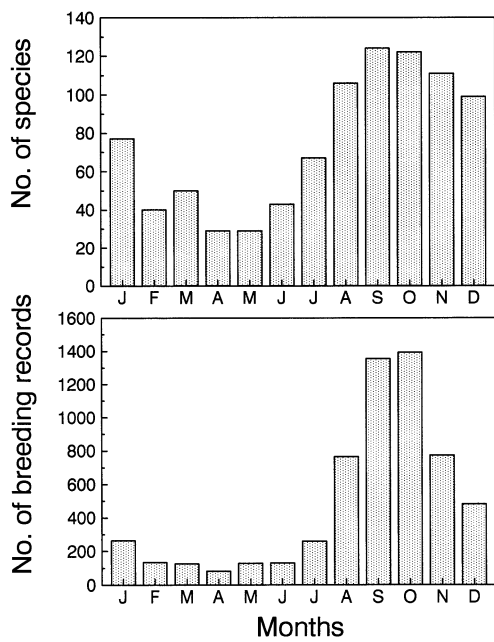


FIG. 8. Numbers of resident species breeding and the number of breeding records each month for the Succulent Karoo.

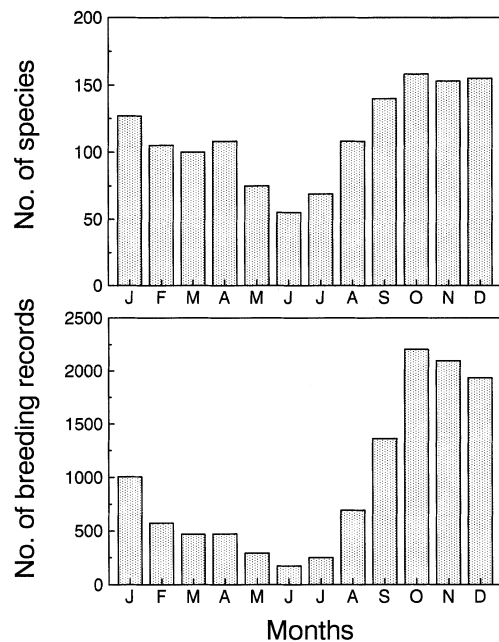


FIG. 9. Numbers of resident species breeding and the number of breeding records each month for the Nama Karoo.

against obstructions. There may be a direct correlation between the productivity of the grassland and the extent to which the sand has been carpeted with awns. The small nomadic granivorous birds all gather nest material from these drifted heaps. These drifts of awns, which are extremely obvious, may provide clear visual evidence of the relative amount of primary production (i.e. the 'quality') of a patch.

Resident species in the Succulent Karoo breed markedly seasonally (Fig. 8), whereas resident species in the Nama Karoo tend to have a longer breeding season, less clearly

defined (Fig. 9). Opportunities for resident species to nest in the Nama Karoo may be irregular because of spatial and temporal variability in resources. Resident species in the Nama Karoo may be adapted for persistence, living at a low density and using every benefit that their territories may offer (such as eating fruit and geophytes if need be; e.g. Broekhuysen, 1963; Dean *et al.*, 1992).

Dryland nomadic species are less constrained by the seasons, and in both the Succulent (Fig. 10) and Nama Karoo (Fig. 11) can breed throughout the year, without a clearly defined 'season'. The nomadic species may have fewer opportunities to breed than residents and probably

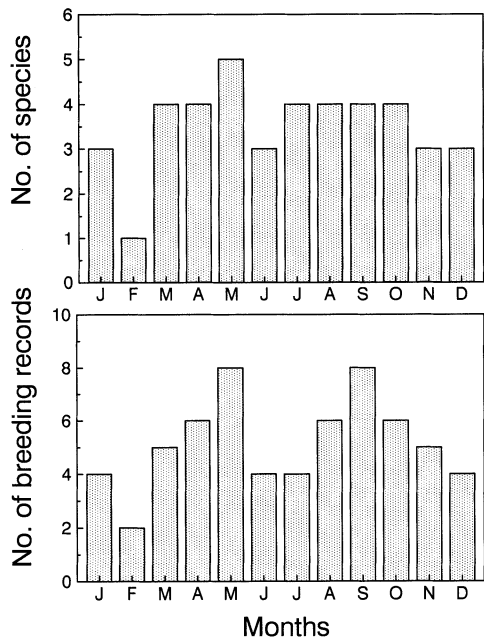


FIG. 10. Numbers of nomadic species breeding and the number of breeding records each month for the Succulent Karoo.

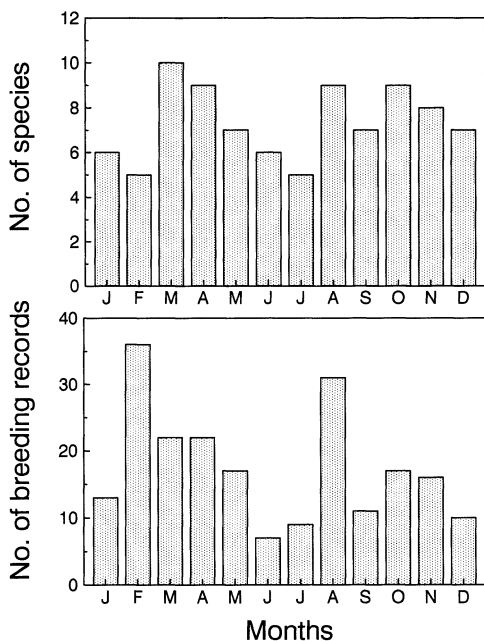


FIG. 11. Numbers of nomadic species breeding and the number of breeding records each month for the Nama Karoo.

have higher productivity from a successful breeding event, but the constraints of a nomadic existence together with relatively high expenditure on reproduction may shorten their life expectancies.

A different breeding strategy is unique to the doublebanded courser *Rhinoptilus africanus* (Temminck) which is insectivorous, locally nomadic, breeds frequently

and at any time of the year, and lays a single egg (Maclean, 1967).

Average clutch sizes do not differ significantly between resident and all nomadic species in the arid and semi-arid Karoo (average clutch size of residents, 3.1 eggs, range 1–10; average clutch size of nomads, 2.5 eggs, range 1–4,  $P=0.08$ , Mann–Whitney  $U$ -test). However, clutch size in several small granivorous lark species, Slater's lark, Stark's lark, greybacked finchlark and blackeared finchlark, probably the most nomadic of all the birds in the Karoo, is significantly smaller than similar-sized, locally nomadic granivorous canaries and buntings, and significantly smaller than the highly nomadic larklike bunting (Dean, 1995).

#### Nomadism as an evolutionary stable strategy

What are the advantages of nomadism? Why should a bird decide to move to a new patch? Or to remain on the old patch? The advantage of an individual bird moving or staying really depends on the variability of the productivity of the environment (Andersson, 1980; Davies, 1984) and on what other members of the population are doing (Sinclair, 1984). If all individuals were resident, then any individual that moved to a new patch would have an initial advantage over the rest of the population, provided that the new patch offered more abundant, or better quality resources. The first birds to move would enjoy less competition from conspecifics, more food, and perhaps escape a build-up of predators at the old patch. The advantage would be short-lived, and would only last until other birds moved to the same patch. The advantage of moving also depends on environmental conditions. In a high rainfall year, when patches are numerous and the probability of finding a high resource patch is high, then moving to a new patch is to the advantage of an individual bird. There is likely to be less competition at the new patch since the total population will be dispersed in many patches. In a low rainfall year, when patches are few and of poor quality, optimal foraging theory predicts that individuals should move only when resource levels are depleted and only when the probability of finding a better patch exceeds the probability of improvement in the current patch. In years when the rainfall is neither high nor low, the probability of improvement in the patch that an individual is occupying is probably equal to the probability of finding a better patch. Furthermore, if rain patches are randomly distributed in time and space, the probability of finding a patch on which rain has recently fallen is equal to the probability of rain falling on the current patch, and there is no advantage in moving regardless of the amount of rain. The decision to stay or move would also be influenced by the numbers of birds that had already moved to or from a patch. As birds leave a patch, there is less competition on the patch, and relatively more food available for the birds that remain, so the probability that the patch will improve increases. Similarly, as birds move into a patch, the probability that the patch will deteriorate increases and the probability of finding a better patch elsewhere will increase.

Nomadism therefore becomes an evolutionary stable strategy for individual species only when extremes in



environmental conditions are frequent enough, and unpredictable enough, to maintain movements to high resource patches or to maintain dispersal away from low resource patches. If high rainfall years are too infrequent, or peaks in fluctuations in the environment too low, or rainfall patches are randomly distributed, nomadism would not be maintained as part of the individual behaviour pattern. If environmental fluctuations are too frequent and regular, the predictability of events would impose regularity in the movements of individuals. Frequent (annual) cyclic fluctuations in the environment will select for migratory, rather than nomadic, movements in birds. The advantage in nomadism really lies in an individual's ability to make the correct decision, on its ability to find a better patch, and its ability to get there ahead of the rest of the population.

It has been suggested by Andersson (1980) that the relative merit of nomadism in birds is higher with cyclic, rather than random, fluctuations in food abundance. Andersson's model indicates that large clutch size, high juvenile survival and low adult survival favour nomadism, and that adult nomadism is favoured as the interval between successive good years increases. Some bird species in the Karoo may fit Andersson's model. With random food production, no particular year is more likely than any other to be 'good' and several good years, or several poor years may occur in succession. In this situation, there are advantages for the birds in being resident, since the probability of finding a better patch than the one that they are in is low. Results from the model thus suggest that cyclic fluctuations in food production will favour the evolution of nomadism in species, whereas random fluctuations will favour site tenacity. Andersson's model, however, is based on assumptions that may be unrealistic, such as that a genotype has the same survival rate whether it is nomadic or resident. The model is further based on a constant ratio between juvenile and adult survival, and does not take into account differential survival in different years. It would be of interest to test the generality of Andersson's model using data for the nomadic larks in the Karoo, but data on survival rates are lacking for this group. There is some evidence that the small granivorous larks in the Nama Karoo would not fit the present model; clutch sizes in this group are small (Dean, 1995) and breeding success is low (Maclean, 1970a).

If there are advantages in being nomadic, why then should some species choose to be resident, or at least relatively sedentary? Nomadic species are generally gregarious, feed mainly on a narrow range of seeds, with some insects (mainly termites), and tend to occur in fairly circumscribed habitats. Resident species tend to be solitary, or in pairs, and to have a fairly mixed diet of insects (including ants), seeds and fruit (pers. obs), and to occur in a fairly wide range of habitats (Maclean, 1993). Therefore, the answer might lie partly in diet and partly in the relative ability of the two groups of species to tolerate fluctuations in habitat quality. The social organization of the two groups of species is more likely to be a consequence of nomadism or of residency than a preadaptation. There is evidently selection for gregariousness in individual nomadic species, but this varies among species (Table 5). There may be advantages in searching for high resource patches by flocks, rather than

TABLE 5. Average size ( $\pm$  standard deviation) of flocks of various nomadic bird species in the southern Karoo.

Species	<i>n</i>	Ave. flock size
Namaqua sandgrouse	41	6.8 ( 3.93)
Redcapped lark	28	8.4 ( 7.57)
Greybacked finchlark	105	35.3 (68.81)
Blackeared finchlark	39	39.8 (40.23)
Larklike bunting	113	30.5 (50.23)

by single birds. This group foraging behaviour is also shown by such resident species as whitebacked and redfaced mousebirds (*Colius colius* (Linnaeus) and *Urocolius indicus* (Latham)), Karoo eremomela (*Eremomela gregalis* (Smith)) and rufouseared warbler (*Malcorus pectoralis* Smith). The energetic cost of moving to find a better patch may be high, and the probability for a solitary bird, or a pair of birds, of finding a new patch may be lower than for a group of birds (Cody, 1971). There are also predation risks which are greater for a solitary bird than a group (Kenward, 1978). The advantages of not moving for a sedentary species might be that a resident would have knowledge of favourable places for foraging and nesting, and would know where the predators were and, presumably, would have some knowledge of predator hunting patterns in its home range (Hinde, 1956). The longer a resident bird remains on its home range, the more its knowledge of the area will improve (Andersson, 1980), and the more costly, in terms of abandoning this knowledge, it is for it to move.

Why do individual birds not adopt the strategy of being nomadic during the good years and resident during the poor years? There is some evidence that all nomadic birds do not move to or from an area (Kieser & Kieser, 1978; Collett, 1982), and there is some evidence that there are regular movements by nomadic or locally nomadic species in southern Africa (James, 1929; Maclean, 1970a, 1970b; Liversidge, 1980; Collett, 1982; Siegfried, 1983; Allan, 1993; Malan, Little & Crowe, 1994). A recent model (Switzer, 1993) that investigated site fidelity suggests that individuals should be 'site faithful' in unpredictable habitats. Furthermore, the success of two decision rules ('always stay' and 'win-stay: lose-switch') suggests that the always stay strategy does well in unpredictable habitats, and that the win-stay: lose-switch strategy does best in predictable habitats (Switzer, 1993). Ultimately, the decision to move or to stay in any locality really depends on what benefits an individual bird will gain. The species and individuals of the nomadic birds in the Karoo may be using different tactics in different years according to the productivity of the environment. If the localities of high resource patches in the Karoo are not randomly dispersed, or are predictable in certain years, then individual nomadic birds are likely to return to them regularly.

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APPENDIX 1. Specific names of all bird species listed in the tables.

- Tawny eagle *Aquila rapax* (Temminck)  
 Blackbreasted snake eagle *Circaetus pectoralis* Smith  
 Lanner falcon *Falco biarmicus* Temminck  
 Ludwig's bustard *Neotis ludwigii* (Rüppell)  
 Burchell's courser *Cursorius rufus* Gould  
 Doublebanded courser *Rhinoptilus africanus* (Temminck)  
 Namaqua sandgrouse *Pterocles namaqua* (Gmelin)  
 Burchell's sandgrouse *Pterocles burchelli* Sclater  
 Namaqua dove *Oena capensis* (Linnaeus)  
 European swift *Apus apus* (Linnaeus)  
 Fawncoloured lark *Mirafra africanoides* Smith  
 Sabota lark *Mirafra sabota* Smith  
 Longbilled lark *Certhilauda curvirostris* (Hermann)  
 Karoo lark *Certhilauda albescens* (Lafresnaye)  
 Red lark *Certhilauda burra* (Bangs)  
 Spikeheeled lark *Chersomanes albofasciata* (Lafresnaye)  
 Redcapped lark *Calandrella cinerea* (Gmelin)  
 Thickbilled lark *Galerida magnirostris* (Stephens)  
 Pinkbilled lark *Spizocorys conirostris* (Sundevall)  
 Sclater's lark *Spizocorys sclateri* (Shelley)  
 Stark's lark *Eremalauda starki* (Shelley)  
 Chestnutbacked finchlark *Eremopterix leucotis* (Stanley)  
 Greybacked finchlark *Eremopterix verticalis* (Smith)  
 Blackeared finchlark *Eremopterix australis* (Smith)
- Sentinel rock thrush *Monticola explorator* (Vieillot)  
 Anteating chat *Myrmecocichla formicivora* (Vieillot)  
 Yellowbellied eremomela *Eremomela icteropygialis* (Lafresnaye)  
 Fantailed cisticola *Cisticola juncidis* (Rafinesque)  
 Chat flycatcher *Melaenornis infuscatus* (Smith)  
 Fairy flycatcher *Stenostira scita* (Vieillot)  
 Wattled starling *Creatophora cinerea* (Meuschen)  
 Malachite sunbird *Nectarinia famosa* (Linnaeus)  
 Lesser doublecollared sunbird *Nectarinia chalybea* (Linnaeus)  
 Greater doublecollared sunbird *Nectarinia afra*  
 Dusky sunbird *Nectarinia fusca* (Vieillot)  
 Black sunbird *Nectarinia amethystina* (Shaw)  
 Cape sparrow *Passer melanurus* (Statius Müller)  
 Scalyfeathered finch *Sporopipes squamifrons* (Smith)  
 Masked weaver *Ploceus velatus* (Vieillot)  
 Redbilled quelea *Quelea quelea* (Linnaeus)  
 Redheaded finch *Amadina erythrocephala* (Linnaeus)  
 Blackthroated canary *Serinus atrogularis* (Smith)  
 Cape canary *Serinus canicollis* (Swainson)  
 Blackheaded canary *Serinus alario* (Linnaeus)  
 Yellow canary *Serinus flaviventris* (Swainson)  
 Whitethroated canary *Serinus albogularis* (Smith)  
 Streakyheaded canary *Serinus gularis* (Smith)  
 Cape bunting *Emberiza capensis* Linnaeus  
 Rock bunting *Emberiza tahapisi* Smith  
 Larklike bunting *Emberiza impetuani* Smith