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Responses of birds to rainfall and seed abundance in the southern Karoo, South Africa

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Resident and nomadic birds, both insectivores and granivores, were counted at 40 sites along a 200-km east–west oval transect in the southern Karoo. Total species richness averaged 30·05 ± 5·31 (S.D.) species per site, with less than half of the species being resident, and nomads and transients making up the remainder. There was a weak correlation between the number of individuals of resident species and rainfall, but no significant correlation between number of individuals of nomadic species and rainfall. The numbers of resident insectivores were significantly correlated with the numbers of arthropods obtained in sweeps. There was no correlation overall between relative seed abundance and numbers and biomass of granivorous nomadic birds, and no correlation between the numbers of resident granivores and the numbers of seeds. The numbers of resident insectivores, resident granivores and nomadic granivores were correlated with the presence and abundance of ephemeral plants at some sites. There was a correlation between the average number of all birds at a site and the proportion of plants that were producing new growth, suggesting that the presence of new growth influences the local abundance of birds.

Keywords: semi-arid; granivory; nomadic birds; shrublands

Introduction

Seasonal changes in habitat structure and food abundance potentially influence the species richness of birds in most terrestrial environments (reviewed by Wiens, 1989). Changes in local species richness of birds may be due to regular seasonal movements by part of any avian species assemblage in any environment that has marked seasonal changes in resource abundance. Where changes in resource levels are not so closely linked to seasonal changes, movements in birds are less regular, and species richness may be less predictable (Dean, 1997). Clear evidence of close tracking of resources has been found in many species of birds from different dietary guilds (Wiens, 1989). Changes in species richness and numbers of granivorous birds with changes in seed abundance in semi-arid habitats have been shown in Chaco, Argentina (Capurro & Bucher, 1982), in the Chihuahuan and Sonoran Deserts, south-western U.S.A. (Brown *et al.*, 1986; Thompson, *et al.*, 1991) and in Kenya, the U.S.A., Brazil and Argentina (Schluter & Repasky, 1991). It follows that nomadic granivorous birds should

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track resources closely, and that there is likely to be a correlation between nomadic bird density and local seed abundance.

The variability of avian species richness and density in semi-arid habitats in South Africa has been observed and discussed by Winterbottom (1968*a*, 1972), Maclean (1970*a*, 1970*b*, 1970*c*, 1970*d*, 1974), Liversidge (1980), Vernon (1986) and Dean (1995). One of the features of semi-arid shrublands, particularly karroid shrublands, is shifts in the number of bird species and their relative abundance in shrubland (Winterbottom, 1968*a*, 1968*b*, 1972); this is thought to be related to local changes in resource quality or quantity. There is little seasonal change in habitat structure in shrublands in the Karoo (Milton, *et al.*, 1992) but long dry periods and irregular rainfall probably affect the local abundance of food and local avian species richness (Dean & Milton, in press). Bird populations in these patches may be limited by resources, and the local species richness of birds may vary in accordance with local shortages or abundances of food (see Wiens, 1989). Since these deficits or surpluses in food are likely to be of short duration, the appropriate response by the avifauna would be movement, thus changing the species richness and the density of birds at a patch (Dean, 1997). The long-term response, in an environment where resources are relatively stable, is that sedentary or resident populations should expand until they became resource-limited. Whether resources are available for extended periods, or whether they are available ephemerally, the structure of avian communities should be such that the overall resource base is exploited most efficiently (Wiens, 1989).

To examine the hypothesis that patchiness in species richness in birds in the Karoo is related to changes in the abundance of food, we regularly collected information on seed abundance, soil surface microarthropods, and bird species richness and abundance at a number of sites in the southern Karoo. Pastoralism is an integral part of present-day Karoo ecosystems, and the effects of different kinds of domestic livestock and the extent to which the shrubland is browsed in a patch may shape the available resources for birds, and thus influence the species of birds that occur in a patch. Although not discussed further here, relevant data on the browsing and grazing effects of domestic livestock on vegetation and birds were collected during the present study and have been discussed elsewhere (Dean, 1995).

Study sites

Data were collected at 40 sites (Table 1) on an east–west transect through karroid shrublands east of Prince Albert, southern Karoo (Fig. 1). The sample sites were on rangelands at 5-km intervals along a roughly oval 200-km route from the Tierberg study site (fully described by Milton *et al.*, 1992), east to Rietbron and back to Tierberg along different roads. The first site was selected by driving 5 km from Tierberg, and then walking 25 m into the shrubland on the left-hand side of the road. The second site was selected by driving 5 km from the first site, and so on until 40 sites had been selected. Some sites chosen in this way were not suitable for various reasons (mostly because of proximity to unusual landscape features, such as an impoundment or drainage line, or a farmhouse) and at these sites we drove a further 1 km and marked our sample site. Sites 1–10, and 31–40 were in the (generally) between-seasons rainfall area, and were in the watershed of the Gamka River. The remainder of the sites were in the (generally) summer rainfall area, and in the watershed of the Sundays River (see Desmet & Cowling, 1999, for a review of climate in the Karoo).

Methods

The current herbivory by domestic livestock on each site was initially estimated (a subjective estimate of whether heavily grazed, moderately grazed or lightly grazed),

Table 1. *Sampling sites in the southern Karoo, South Africa. Site 1 is 5 km east of Tierberg farm house, and site 20 just west of Rietbron*

Site	Topography	Soil	Vegetation, cover (%), ht (cm)
Western sites			
1	Plain	Silt	Dwarf shrubland, 35, < 50
2	Plain	Silt	Dwarf shrubland, 35, < 50
3	Plain	Silt	Dwarf shrubland, 40, < 50
4	Plain	Silt	Dwarf shrubland, < 40, < 50
5	Plain	Sandy	Dwarf shrubland, < 40, < 30
6	Flat ridge top	Shale	Dwarf shrubland, < 20, < 20
7	Gentle slope	Shale	Dwarf shrubland, < 20, *ca.* 20
8	Gentle slope	Shale	Dwarf shrubland, 30, *ca.* 30
9	Gentle slope	Shale	Dwarf shrubland, 30, *ca.* 40
10	Stony plain	Shale	Dwarf shrubland, 20, *ca.* 30
31	Gentle slope	Shale	Dwarf shrubland, 25, 40–50
32	Plain	Silt	Dwarf shrubland, 15, *ca.* 40
33	Undulating	Sandy	Dwarf shrubland, 20, *ca.* 30
34	Plain	Sandy	Dwarf shrubland, 25, *ca.* 35
35	Stony ridge	Shale	Dwarf shrubland, 25, *ca* 30
36	Stony ridge	Shale	Dwarf shrubland, 30, *ca.* 30
37	Plain	Sandy	Dwarf shrubland, 35, *ca.* 30
38	Plain	Sandy	Dwarf shrubland, 35, *ca.* 25
39	Gentle slope	Sandy	Dwarf shrubland, 25, *ca.* 30
40	Plain	Sandy	Dwarf shrubland, 20, *ca.* 40
Eastern sites			
11	Flat ridge top	Shale	Dwarf shrubland, 30, *ca.* 30
12	Plain	Shale	Dwarf shrubland, 35, *ca.* 30
13	Gentle slope	Shale	Dwarf shrubland, 20, 20–100
14	Undulating	Shale	Dwarf shrubland, 30, 40–60
15	Plain	Shale	Dwarf shrubland, 20, 20–60
16	Plain	Sandy	Grassy dwarf shrubland, 40 < 50
17	Plain	Sandy	Dwarf shrubland, 30, *ca.* 20
18	Flood plain	Clay	Shrubland, 25, 1–3 m
19	Plain	Shale	Dwarf shrubland, 30, *ca.* 40
20	Plain	Shale	Dwarf shrubland, 40, *ca.* 40
21	Plain	Silt	Dwarf shrubland, 20, ~ 25
22	Plain	Sandy	Dwarf shrubland, 30, *ca.* 40
23	Plain	Sandy	Dwarf shrubland, 10, *ca.* 40
24	Plain	Sandy	Dwarf shrubland, 25, *ca.* 40
25	Plain	Shale	Grassy dwarf shrubland, 25, *ca.* 30
26	Plain	Shale	Grassy dwarf shrubland, 15, *ca.* 20
27	Plain	Shale	Grassy dwarf shrubland, 25, *ca.* 40
28	Plain	Sandy	Dwarf shrubland, 15, *ca.* 20
29	Plain	Silt	Dwarf shrubland, 25, *ca.* 20
30	Stony plain	Sandy	Dwarf shrubland, 20, *ca.* 15

basing the evaluation of current grazing or browsing effects on the extent to which grass and shrubs had been hedged. The dominant plant species were identified, plant cover was estimated and average plant height was measured at each site. Thereafter, on

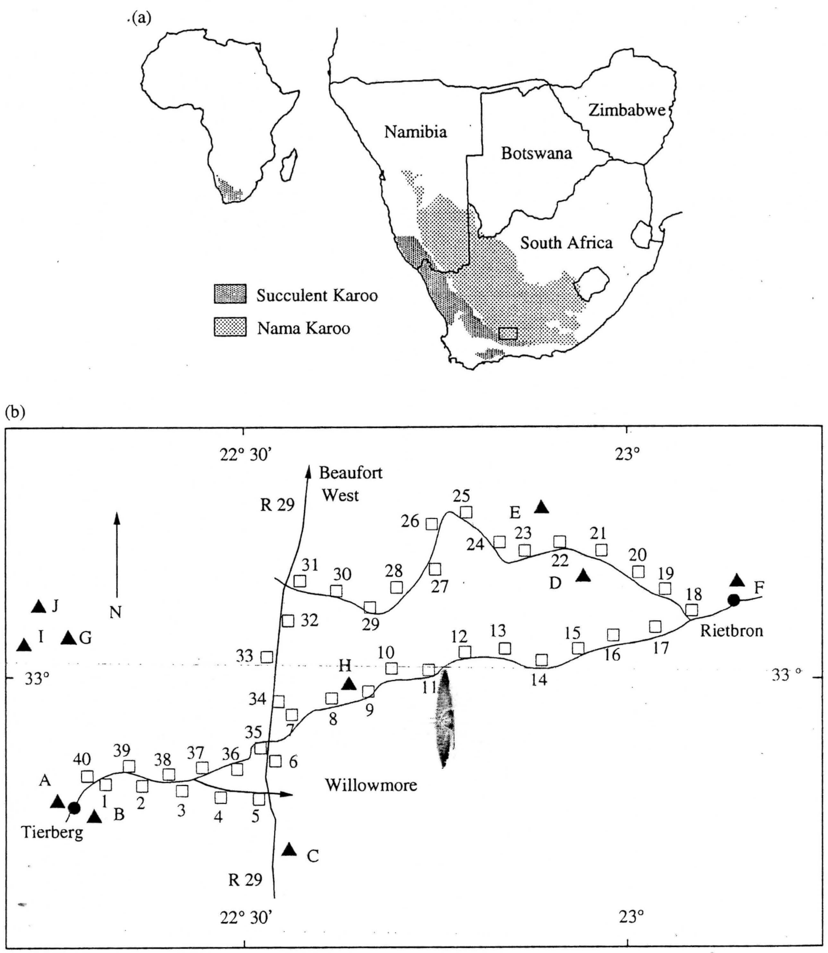

Figure 1. (a) Southern Africa, showing the relative position of the Karoo on the African continent, and the area (block near the south-western edge of the Karoo) where the study was undertaken. (b) An enlargement of this area, showing the study sites (numbered squares) and rainfall stations (solid triangles).

one day of each month from January 1988 to December 1990 (with the exception of October 1989), we identified all bird species within a radius of 50 m of the site, and for 5 min counted all individuals of all species of birds within that area (excluding birds flying over the site). All bird species were classified as resident, nomad, local nomad or transient (see Results). Nomads are those species whose occurrence at a site is irregular, both seasonally and year to year, and that are nomadic on a regional scale; the species is usually either present in numbers, or absent completely (Sinclair, 1984; Dean, 1997). Local nomads are those species that form flocks when not breeding and that wander locally, and a few individuals are often present at any site, but numbers vary. Transients were those that were either recorded once only during the 3 years of the study, or species

that have large territories, of which the site may have been a small fraction. Avian biomass at each site was calculated from data on the mass of species given by Maclean (1993).

Seeds and microarthropods on the soil surface were sampled by running a 12-V vacuum cleaner (with mouth 33-mm wide × 5-mm deep) for 30 s across the soil in the open between shrubs and for a further 30 s across the soil below the canopy shadow of shrubs. This provided a measure of the density of seeds and of microarthropods on the soil surface. The samples (sweeps) collected in this way were up to 15 g of a soil/seed/microarthropod mixture per 30 s sweep (i.e. up to 30 g per site), and for the whole transect an average of 23·6 ± 4·6 g of soil/seed mixture per site per month was collected and sorted.

The species richness and abundance of ephemeral plants was observed and estimated at each site, and the phenology of perennial and short-lived perennial plants was sampled by examining a variety of species and classifying them as dormant, growing, flowering or fruiting.

Data on rainfall for weather stations close to our sites were obtained from the South African Weather Bureau, Pretoria. The rainfall stations were divided into five groups according to their localities in relation to the sites. For groups that contained more than one rainfall station, the mean rainfall for the group was used. Rainfall data collected at the Tierberg study site (Milton *et al.*, 1992) and at the nearby Tierberg farm house were used for sites 1–4 and 36–40 (Table 2).

These data were analysed statistically using regressions to correlate the numbers of both resident and nomadic species at each site with rainfall, and the abundance of microarthropods, seeds and ephemeral plants. The possible relationship between rainfall and seeds, and rainfall and bird abundance was tested in two ways. A series of regressions using current rainfall ($Rain_0$) was run, and this was followed by a second set of regressions relating to the rainfall in the previous month or months ($Rain_n$).

Results

Species richness, numbers and biomass of birds

Total species richness, including residents, nomads and transient species, ranged from 20 to 46 bird species per site (mean species richness 30·05 ± 5·31 per site). Less than half of the species recorded at most sites were considered to be resident at that site, with nomads and transients making up the remainder. Resident species or nomads foraging or breeding at the sites are given in Table 3 and transient species are detailed in Table 4. Transient species were excluded from all site analyses of abundance and biomass. Those transients present at many of the sites included Pale Chanting Goshawk *Melierax canorus*, Greater Kestrel *Falco rupicoloides*, Karoo Korhaan *Eupodotis vigorsii*, Cape Crow *Corvus capensis*, and Pied Crow *C. albus*.

The species richness, numbers and biomass of birds varied at most sites, both among residents (Fig. 2) and nomads (Fig. 3). Residents were both more abundant and showed more variation in numbers and biomass at the western sites (Sites 1–9, 34–40) than at the eastern sites, but there was generally more variation in the numbers and biomass of nomads at the eastern sites (Sites 10–33). Nomads usually far out-numbered residents and generally made up the bulk of the biomass at most sites where they occurred. The numbers of individuals and species richness of residents and nomads had a high variance at the majority of sites, suggesting that there are some movements in residents (if only very local) and that the species richness (and biomass) of the avifauna in these shrublands is not static. However, resident species did not show the extreme pattern of fluctuating abundance that was shown by the nomads at the same sites, and there was no correlation between the numbers of residents and the number of nomads at all sites

Table 2. *Total annual rainfall for sites along or in the general area of the transect. Letters after the name of the station identify the position of the station on the map (Fig. 1(b))*

Locality	Total annual rainfall (mm)			Co-ordinates
	1988	1989	1990	
Tierberg site (A)	270	252	156	33°08′ S; 22°17′ E
Tierberg farm (B)	286	245	193	33°15′ S; 22°16′ E
Rondawel (C)	138	157	116	33°12′ S; 22°43′ E
Aardoorns (D)	167	166	179	32°50′ S; 22°56′ E
Klipkrans (E)	173	299	105	32°45′ S; 22°55′ E
Rietbron (F)	192	249	122	32°54′ S; 23°09′ E
Rietfontein (G)	186	245	220	32°55′ S; 22°21′ E
Lammerkraal 1 (H)	168	211	133	33°02′ S; 22°36′ E
Lammerkraal 2 (I)	148	212	150	32°50′ S, 22°19′ E
Knapdraai (J)	185	147	130	33°46′ S; 22°17′ E

(resident insectivores *vs.* nomads, $r^2 = 0{\cdot}01$; resident granivores *vs.* nomads, $r^2 = 0{\cdot}026$, both NS) suggesting that the two groups were responding to different environmental cues. It was also noted that some sites always had very few individual birds and species, and were seldom, if ever, visited by the flocks of nomads that were observed at other sites.

Table 3. *Species considered to be resident, nomadic (*) or locally nomadic (†) at the study sites, ranked in order of number of sites at which they were recorded. Species recorded breeding at a study site or near (within 100 m) of a site are in bold type*

Species	Food	No. of sites
Rufous-eared Warbler *Malcorus pectoralis* Smith	I	40
Karoo Chat *Cercomela schlegelii* (Wahlberg)	I	40
Long-billed Lark *Certhilauda curvirostris* (Hermann)	M	40
Spike-heeled Lark *Chersomanes albofasciata* (Lafresnaye)	M	40
Cape Sparrow *Passer melanurus* (Statius Müller)	M	39
†**Yellow Canary** *Serinus flaviventris* (Swainson)	G	38
***Lark-like Bunting** *Emberiza impetuani* Smith	G	38
Thick-billed Lark *Galerida magnirostris* (Stephens)	M	36
***Black-headed Canary** *Serinus alario* (Linnaeus)	G	32
***Red-capped Lark** *Calandrella cinerea* (Gmelin)	M	30
***Grey-backed Finchlark** *Eremopterix verticalis* (Smith)	G	30
†**Chat Flycatcher** *Melaenornis infuscatus* (Smith)	I	30
†**White-throated Canary** *Serinus albogularis* (Smith)	G	30
Bokmakierie *Telophorus zeylonus* (Linnaeus)	I	29
*Namaqua Sandgrouse *Pterocles namaqua* (Gmelin)	G	27
Fiscal Shrike *Lanius collaris* Linnaeus	I	27
Tractrac Chat *Cercomela tractrac* (Wilkes)	I	22

Table 3—*Continued.*

Species	Food	No. of sites
African Pipit *Anthus cinnamomeus* (Gmelin)	I	21
Karoo Lark *Certhilauda albescens* (Lafresnaye)	M	20
Cape Bunting *Emberiza capensis* Linnaeus	G	20
Grey-backed Cisticola *Cisticola subruficapilla* (Smith)	I	17
Karoo Eremomela *Eremomela gregalis* (Smith)	I	16
Red-faced Mousebird *Urocolius indicus* (Latham)	F	16
Southern Grey Tit Parus afer Gmelin	I	16
Spotted Prinia *Prinia maculosa* (Boddaert)	I	14
Cape Penduline Tit *Anthoscopus minutus* (Shaw and Nodder)	I	14
Cape Turtle Dove *Streptopelia capicola* (Sundevall)	G	13
†**Namaqua Dove** *Oena capensis* (Linnaeus)	G	12
Southern Ant-eating Chat *Myrmecocichla formicivora* (Vieillot)	I	10
Dusky Sunbird *Nectarinia fusca** (Vieillot)	N	10
Pied Barbet *Tricholaema leucomelas* (Boddaert)	F	10
Familiar Chat *Cercomela familiaris* (Stephens)	I	10
Yellowbellied Eremomela *Eremomela icteropygialis** (Lafresnaye)	I	10
Pied Starling *Spreo bicolor* (Gmelin)	I + F	9
Black-eared Finchlark *Eremopterix australis** (Smith)	G	9
†Malachite Sunbird *Nectarinia famosa* (Linnaeus)	N	9
Southern Masked-Weaver *Ploceus velatus* Vieillot	M	8
†**Southern Double-collared Sunbird** *Nectarinia chalybea* (Linnaeus)	N	7
Karoo Scrubrobin *Cercotrichas coryphaeus* (Lesson)	I	6
Chestnut-vented Titbabbler *Parisoma subcaeruleum* (Vieillot)	I	6
Long-billed Crombec *Sylvietta rufescens* (Vieillot)	I	5
Plain-backed Pipit *Anthus leucophrys* Vieillot	I	5
*Wattled Starling *Creatophora cinerea* (Meuschen)	I + F	5
†**Double-banded Courser** *Smutsornis africanus* (Temminck)	I	4
Diederik Cuckoo *Chrysococcyx caprius* (Boddaert)	I	4
Pririt Batis *Batis pririt* (Vieillot)	I	3
†**Fairy Flycatcher** *Stenostira scita* (Vieillot)	I	3
***Scaly-feathered Finch** *Sporopipes squamifrons* (Smith)	G	3
***Red-headed Finch** *Amadina erythrocephala* (Linnaeus)	G	3
Layard's Titbabbler *Parisoma layardi* Hartlaub	I	2
Red-eyed Bulbul *Pycnonotus nigricans* (Vieillot)	F	2
Mountain Wheatear *Oenanthe monticola* Vieillot	I	2
White-backed Mousebird *Colius colius* (Linnaeus)	F	2
Southern Grey-headed Sparrow *Passer diffusus* (Smith)	M	2
*Red-billed Quelea *Quelea quelea* (Linnaeus)	G	2

Food categories are: F = fruit, G = granivore, I = invertebrates (most species listed include juicy fruits in their food), M = mixed invertebrates and seeds, N = nectar (all species listed include invertebrates in their food), O = omnivore (food includes vertebrates, invertebrates, seeds, juicy fruits, flowers, buds and growing shoot tips), R = raptor.

Table 4. *Species considered to be transient on sampling sites, ranked in order of number of sites at which they were recorded. Food categories given in Table 3*

Species	Food	No. of sites
Karoo Korhaan *Eupodotis vigorsii* (Vieillot)	O	40
Cape Crow *Corvus capensis* Lichtenstein	O	40
Ludwig's Bustard *Neotis ludwigii* (Rüppell)	O	33
Barn Swallow *Hirundo rustica* Linnaeus	I	32
Pale Chanting Goshawk *Melierax canorus* (Thunberg)	R	20
Greater Kestrel *Falco rupicoloides* Smith	R	19
Pied Crow *Corvus albus* Statius Müller	O	10
Eurasian Swift *Apus apus* (Linnaeus)	I	8
Rock Kestrel *Falco tinnunculus* Linnaeus	R	7
Kori Bustard *Ardeotis kori* (Burchell)	O	7
Speckled Pigeon *Columba guinea* Linnaeus	G	7
Southern Black Korhaan *Eupodotis afra* (Linnaeus)	O	6
Lesser Kestrel *Falco naumanni* Fleischer	I	4
Crowned Lapwing *Vanellus coronatus* (Boddaert)	I	4
Greater Striped Swallow *Hirundo cucullata* Boddaert	I	4
Rock Martin *Hirundo fuligula* Lichtenstein	I	4
Martial Eagle *Polemaetus bellicosus* (Daudin)	R	3
Little Swift *Apus affinis* (Gray)	I	3
Alpine Swift *Tachymarptis melba* (Linnaeus)	I	3
European Bee-eater *Merops apiaster* Linnaeus	I	3
Whiterumped Swift *Apus caffer* (Lichtenstein)	I	2
Egyptian Goose *Alopochen aegyptiacus* (Linnaeus)	G	2
Yellow-billed Duck *Anas undulata* Dubois	G	2
Secretarybird *Sagittarius serpentarius* (Miller)	R	2
Pied Avocet *Recurvirostra avosetta* Linnaeus	I	2
Spotted Thick-knee *Burhinus capensis* (Lichtenstein)	I	2
Verreaux's Eagle *Aquila verreauxii* Lesson	R	1
Red-breasted Sparrowhawk *Accipiter rufiventris* Smith	R	1
Three-banded Plover *Charadrius tricollaris* Vieillot	I	1
Black-winged Stilt *Himantopus himantopus* (Linnaeus)	I	1
Burchell's Courser *Cursorius rufus* Gould	I	1
Red-eyed Dove *Streptopelia semitorquata* (Rüppell)	G	1
Speckled Mousebird *Colius striatus* Gmelin	F	1
African Hoopoe *Upupa africana* Bechstein	I	1
Clapper Lark *Mirafra apiata* (Vieillot)	M	1
Sclater's Lark *Spizocorys sclateri* (Shelley)	M	1
White-throated Swallow *Hirundo albigularis* Strickland	I	1
Plain Martin *Riparia paludicola* (Vieillot)	I	1
White-necked Raven *Corvus albicollis* Latham	O	1
Capped Wheatear *Oenanthe pileata* (Gmelin)	I	1
Sickle-winged Chat *Cercomela sinuata* (Sundevall)	I	1
Fiscal Flycatcher *Sigelus silens* (Shaw)	I	1
Pale-winged Starling *Onychognathus nabouroup* (Daudin)	I + f	1
Southern Red Bishop *Euplectes orix* (Linnaeus)	G	1

Resources, bird numbers and rainfall

The seasonal pattern in the rainfall over the 3 years was not very marked, although rain events tended to occur during the autumn and spring in the western sites and in summer

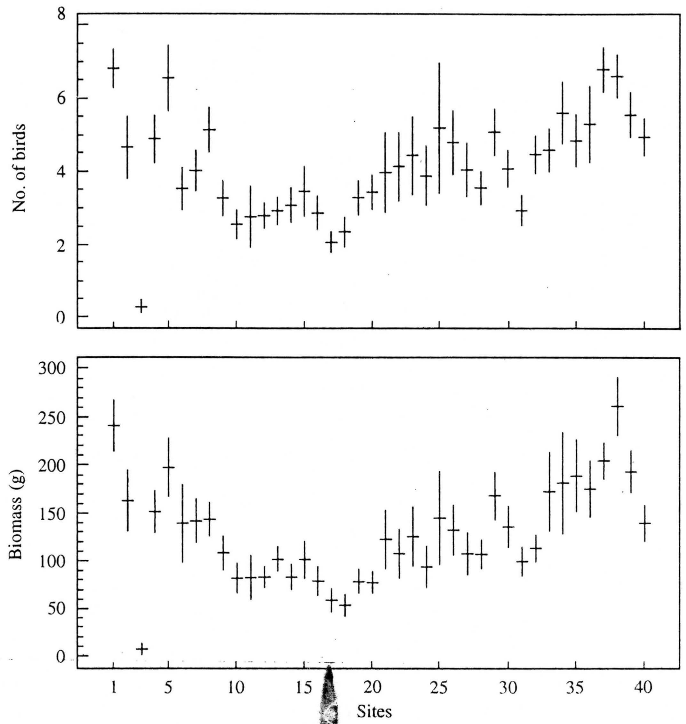

Figure 2. Average numbers and biomass of all resident birds at study sites. The average number is shown by the horizontal bar, while the vertical bar shows ± 1 standard error (S.E.).

in the eastern sites. Rainfall in both the western and eastern sites was highly variable from month to month and from year to year (Fig. 4, Table 2). Total rainfall during the 3 years differed within and between sites, and showed a general trend of decreasing annual rainfall from 1988 to 1990 at some sites (Table 2).

There was no correlation between the number of arthropods collected per sweep and current rainfall (Rain$_0$: $r^2 = 0{\cdot}001$). However, the number of arthropods was significantly correlated with the amount of rain during the previous month (Rain$_1$: $r^2 = 0{\cdot}02$, $p < 0{\cdot}001$), but not with rain 2 months before.

There was no correlation between the mean monthly density of seeds on the soil surface and rainfall (Rain$_0$: $r^2 = 0{\cdot}008$; Rain$_1$: $r^2 = 0{\cdot}007$). The number of seeds collected per plot was variable, but in general seeds were more abundant (with a higher variance) in the eastern sites (Fig. 5). Seeds showed a general pattern of highest abundance over the whole area of the study in late winter and spring 1988 (Fig. 6).

Similarly, there was no correlation between the number of resident birds and rainfall (Rain$_0$: $r^2 = 0{\cdot}008$; Rain$_1$: $r^2 = 0{\cdot}02$), and no significant correlation between nomadic birds and rainfall (Rain$_0$: $r^2 = 0{\cdot}002$; Rain$_1$: $r^2 = 0{\cdot}0002$).

Bird numbers and microarthropod abundance

The numbers of individuals of resident insectivore species were significantly correlated with the numbers of arthropods obtained in sweeps ($r^2 = 0{\cdot}02$, $p < 0{\cdot}001$).

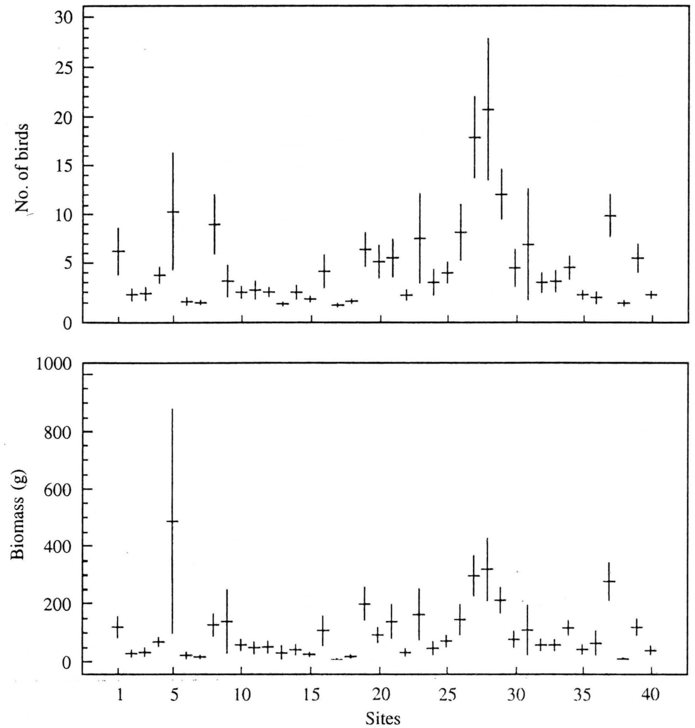

Figure 3. Average numbers and biomass (± 1 S.E.) of all nomadic species at study sites.

Bird numbers and relative seed abundance

In general there was no correlation overall between the amount of seeds collected in sweeps and the numbers and biomass of granivorous nomadic birds (numbers: $r^2 = 0{\cdot}004$, NS; biomass: $r^2 = 0{\cdot}001$, NS). However, if sites where no birds were observed on more than four occasions were removed from the database, the correlation between seed numbers and numbers of nomadic birds is significant ($r^2 = 0{\cdot}11$, $p < 0{\cdot}001$). There was also no correlation between the numbers of resident granivores and the numbers of seeds ($r^2 = 0{\cdot}003$, NS), and again the correlation was significant if the consistent zero bird sites were removed from the database ($r^2 = 0{\cdot}17$, $p = 0{\cdot}048$).

Bird numbers and ephemeral plant abundance

The numbers of resident insectivores, resident granivores and nomadic granivores were not correlated with the presence or abundance of ephemeral plants at all sites. However, if the consistent zero birds sites are removed from the database, the correlation between the numbers of nomadic granivores and the number of ephemeral plants is statistically significant ($r^2 = 0{\cdot}09, p < 0{\cdot}001$), but not significant between residents and the numbers of ephemeral plants.

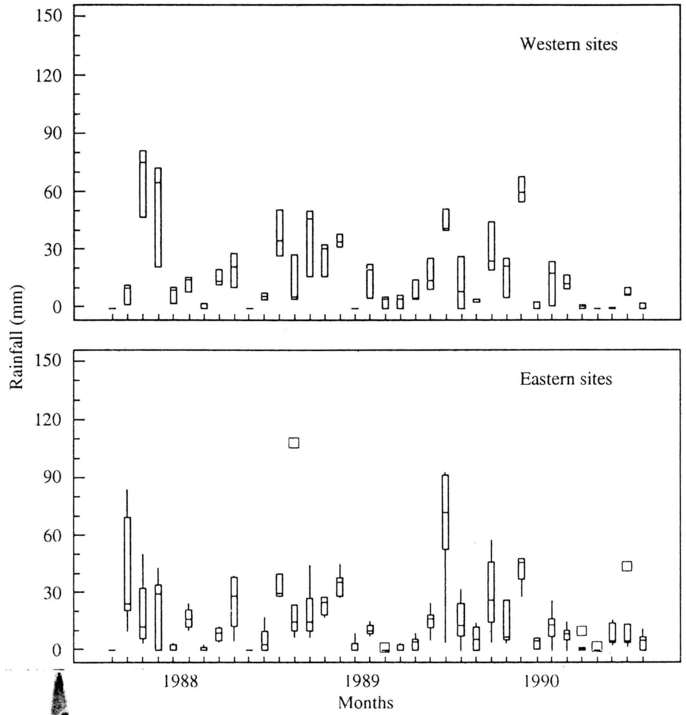

Figure 4. A 'box-and-whisker' plot showing the average rainfall each month for sites in the western and eastern parts of the transect. The 'box' covers the central 50% of the values, and the 'whiskers' show the range of the data.

Bird numbers and growing plants

The presence of new growth on the plants may be a cue to birds that not only had the shrubland recently received rain, but that other resources, such as populations of invertebrates and the seeds of annual plants were available. There was a significant correlation between the average number of all birds at a site, and the proportion of plants that were producing new growth ($r^2 = 0{\cdot}16$, $p = 0{\cdot}01$) (Fig. 7). This relationship was not significant between nomadic birds and growing plants, although the similar curve suggests that there is some response by nomadic birds to the higher proportion of new growth in the plants (Fig. 8). There was a weak and non-significant correlation between the numbers of resident species and new growth.

Breeding of nomadic birds

There was only one major breeding attempt by nomadic birds in 3 years. In August 1988, about 20 pairs of Grey-backed Finchlarks, *Eremopterix verticalis*, 2 pairs of Black-eared Finchlarks, *E. australis*, and about 20 pairs of Lark-like Buntings, *Emberiza impetuani*, nested in grassy dwarf shrubland at sites 25, 26 and 27. Although this breeding event was not correlated with rain or with high numbers of seeds at these sites,

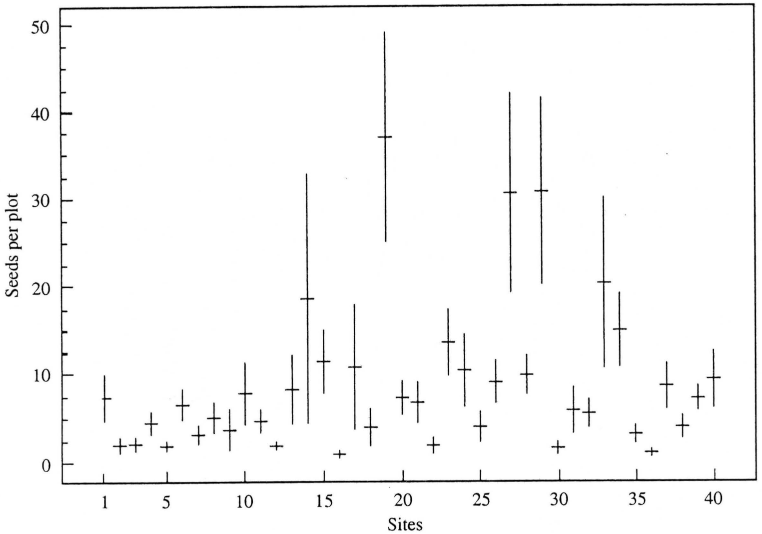

Figure 5. The average (± 1 S.E.) of seeds collected per sweep at each study site during 1988–1990.

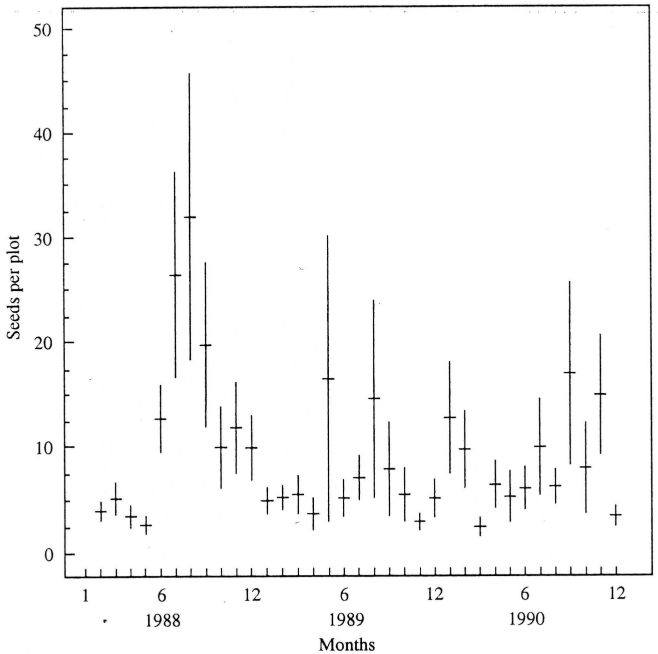

Figure 6. The average (± 1 S.E.) of seeds collected each month from 1988–1990, all sites combined. Note: no data for October 1989.

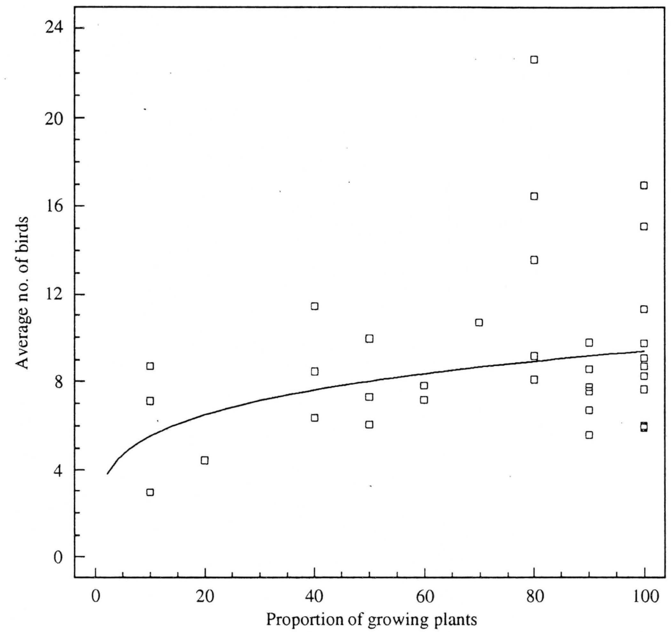

Figure 7. A regression of the average number of resident birds per site against the proportion of growing plants. The line has the equation $y = 2{\cdot}24 \times 0{\cdot}234$ ($r^2 = 0{\cdot}16$, $p = 0{\cdot}01$). Plant data have been arc-sine transformed.

it did coincide with the period in which the highest numbers of seeds were recorded for the whole area (Fig. 6).

Responses of individual species

The responses of individual species are masked in the above analyses, and it is informative to examine the movements of common resident and nomadic species. The average numbers of three resident species recorded consistently at all sites (Long-billed Lark, *Certhilauda curvirostris*, Karoo Chat, *Cercomela schlegelii*, and Rufous-eared Warbler, *Malcorus pectoralis*) are shown in Fig. 9, and the average numbers of three nomadic species (Namaqua Sandgrouse, *Pterocles namaqua*, Grey-backed Finchlark, and Lark-like Bunting) and three locally nomadic species (Namaqua Dove, *Oena capensis*, Yellow Canary, *Serinus flaviventris*, and White-throated Canary, *S. albigularis*) are shown in Fig. 10 and Fig. 11, respectively. The numbers of all three resident species were fairly consistent throughout the year, but all three showed a slight increase in late summer, probably due to the presence of immatures after the breeding season from August to November. Both nomads and local nomads, however, showed inconsistent patterns, both seasonally and annually, and between species. There is some evidence that movements of the Namaqua Sandgrouse may follow a regular pattern, but a time-series analysis (autocorrelation) of these data is not significant. In the Grey-backed Finchlark and Lark-like Bunting, movements are clearly irregular, both seasonally and annually, and the species further differ from each other in the time of year when they are

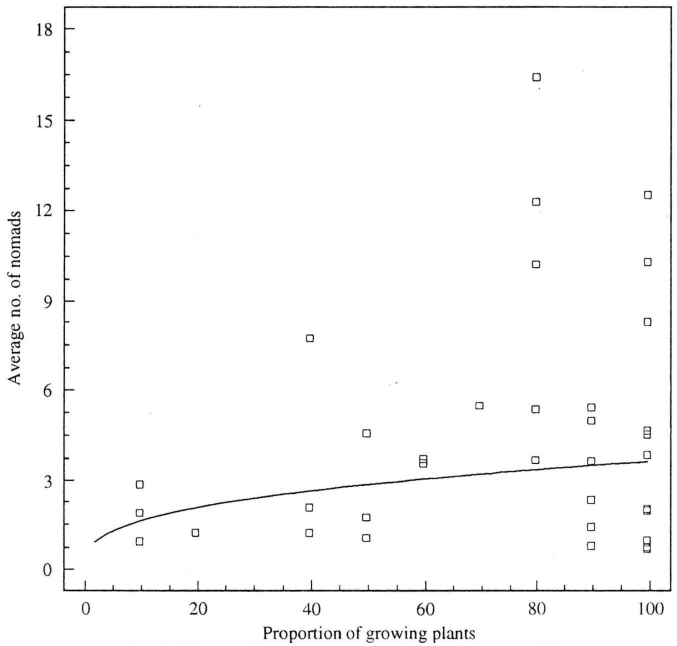

Figure 8. A regression of the average number of nomadic birds per site against the proportion of growing plants. The line has the equation $y = 1{\cdot}28 \times 0{\cdot}367$ and is not significant ($r^2 = 0{\cdot}07$). Plant data have been arc-sine transformed.

present in the area, suggesting that they are responding to different environmental cues. The numbers of Namaqua Sandgrouse, Grey-backed Sparrowlark and Lark-like Bunting were not correlated with the number of seeds per plot or rainfall overall. The local nomads present a rather more complex picture. Namaqua Doves are seasonal migrants into the southern Karoo and are locally nomadic but seldom abundant within the area (well illustrated in Fig. 11). Yellow Canaries and White-throated Canaries are locally nomadic and form small flocks at any time of year. Figure 11 shows this very well, and also shows that flocking was more prevalent in the drier years (1989, 1990).

To show site use by the same set of species, the average number of birds per site was plotted (Figs. 12, 13 and 14). Once again the resident species showed consistent patterns and were present at all sites in approximately the same numbers. Both nomads and local nomads showed a preference for certain sites, although this is less evident in the Yellow Canary than in the other species. What is of interest is that the nomads showed very little overlap in site preference.

Discussion

Optimal foraging theory predicts that an increase in the amount of resources should lead to an increase in the total number of birds if the resources are available for long enough for the birds to show a demographic response. In the short-term, a high resource patch

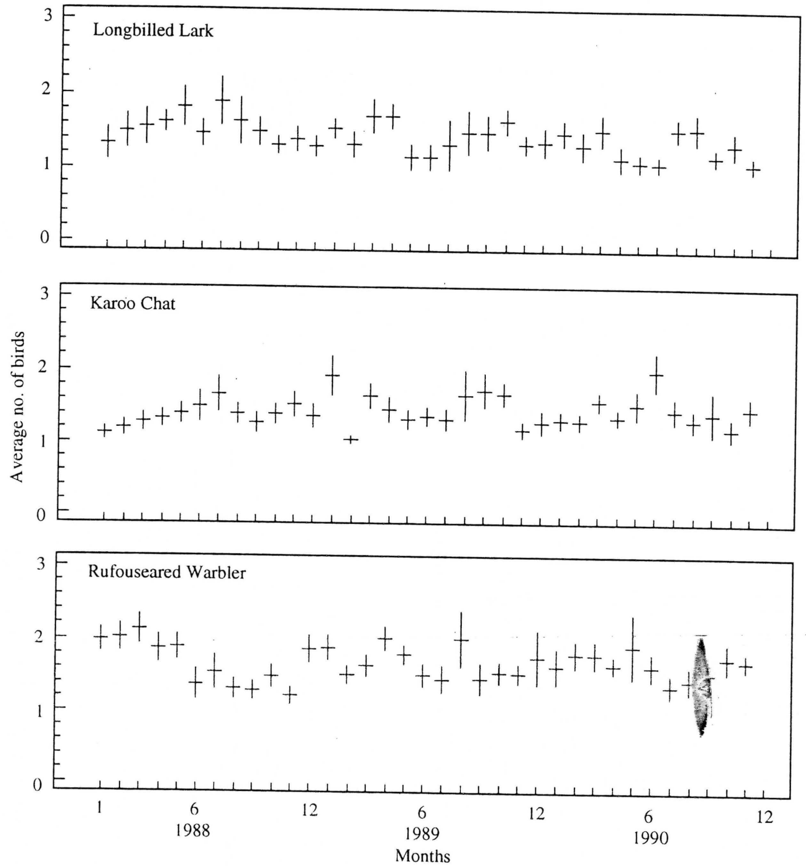

Figure 9. Average ($\pm$ 1 S.E.) number of selected resident species each month, all sites combined. Note: no data for October 1989.

should attract birds, leading to an increase in the number of birds on the patch. Neither this study, nor other recent studies (e.g. Repasky & Schluter, 1994) support this unconditionally. However, as Wiens (1989) has pointed out 'what we witness in nature may at times only coarsely fit the optimal states expected from theory'. At best, the findings of our study can only be described as coarsely fitting the hypothesis that patchiness in species richness in birds in the Karoo is related to changes in the abundance of food.

However, we do show some results relating to the stability of species richness that have not been documented in any previous study of birds in the Karoo (although movements and stability of avifauna has been alluded to by Winterbottom (1968*a*), Siegfried (1983) and Vernon (1986)). (1) Resident birds in the Karoo appear to be subject to local movements, even if these be only a few hundred metres, and (2) The occurrence of nomadic species at any site in the study area was unpredictable in time and space, suggesting that different species of nomadic birds may be responding to

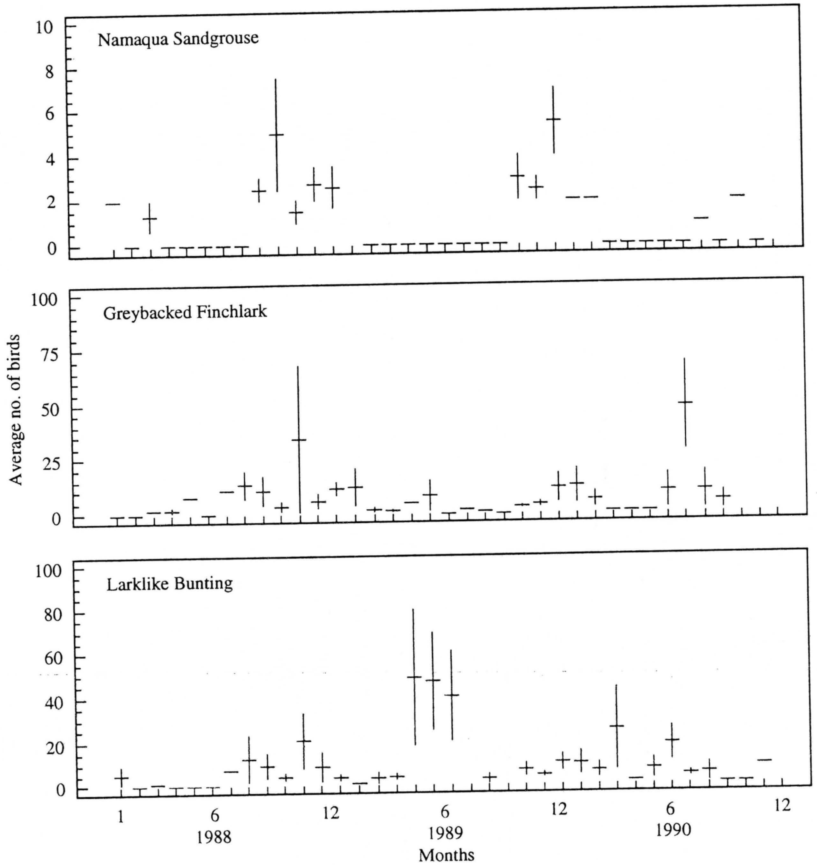

Figure 10. Average (± 1 S.E.) number of selected nomadic species each month, all sites combined. Note: no data for October 1989.

different environmental cues. The study also shows that resource levels, both seeds and arthropods, are not constant. We were unable to correlate the numbers of nomadic birds with measured amounts of seed or with rainfall, and it seems likely that the presence or absence of birds at any particular site is not only influenced by the variable level of resources, but also by conditions elsewhere.

The response of birds to new growth on the plants perhaps indicates to the birds that shrublands have reached a certain productive state following rain. This productive state may carry with it an increase in the numbers of invertebrates, fruits and seedlings. Termites *Hodotermes mossambicus* increase foraging activity on the soil surface when grass growth increases (Coaton, 1958) and the smaller *Microhodotermes viator* of the southern Karoo has a tendency to forage after rain, though their foraging activities are generally unpredictable (Dean, 1993). Termites are eaten by a large number of bird species (Brooke *et al.*, 1972; Kok & Hewitt, 1990), and their activities may influence the species richness and numbers of birds at a patch. We suggest that nomadic birds move

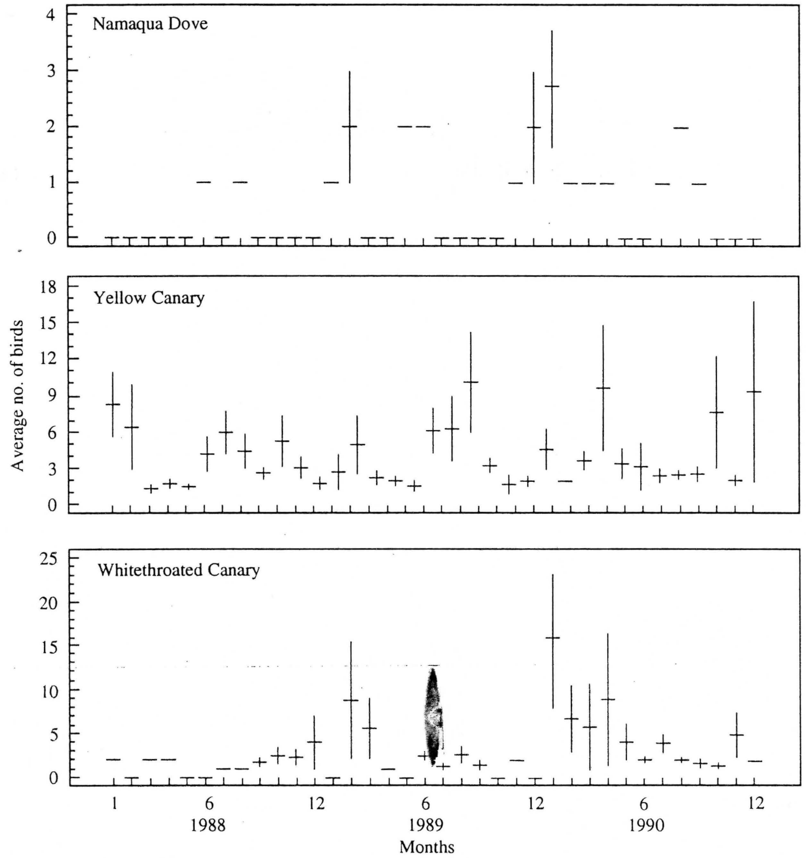

Figure 11. Average (± 1 S.E.) number of selected locally nomadic species each month, all sites combined. Note: no data for October 1989.

into an area after the flush of new growth, timing their arrival to coincide with ripening seed. Both summer and winter growing annual plants respond rapidly to rainfall; germinating, growing and setting seed within 6–12 weeks (Rösch, 1977). Their seeds, which are produced more abundantly than those of perennial plants, are not available to birds until the annuals die and dry out. Grasses may respond even more rapidly (pers. obs). So lags between rain, the presence of abundant seeds, and the appearance and breeding of nomadic granivorous birds are to be expected.

Data on the temporal and spatial stability of common resident species suggest that although there may be local movements in these birds, and small increases in abundance due to young birds entering the population, the birds are largely sedentary. Nomadic species lack stability, and show gross changes in numbers of individuals, both spatially and temporally. Unlike residents, or the locally nomadic Yellow Canary, nomadic species did not use all sites equally, and showed a marked presence at certain sites, although this presence differed between sites in different years. It may be significant that the two commonest nomad species (Grey-backed Finchlark and

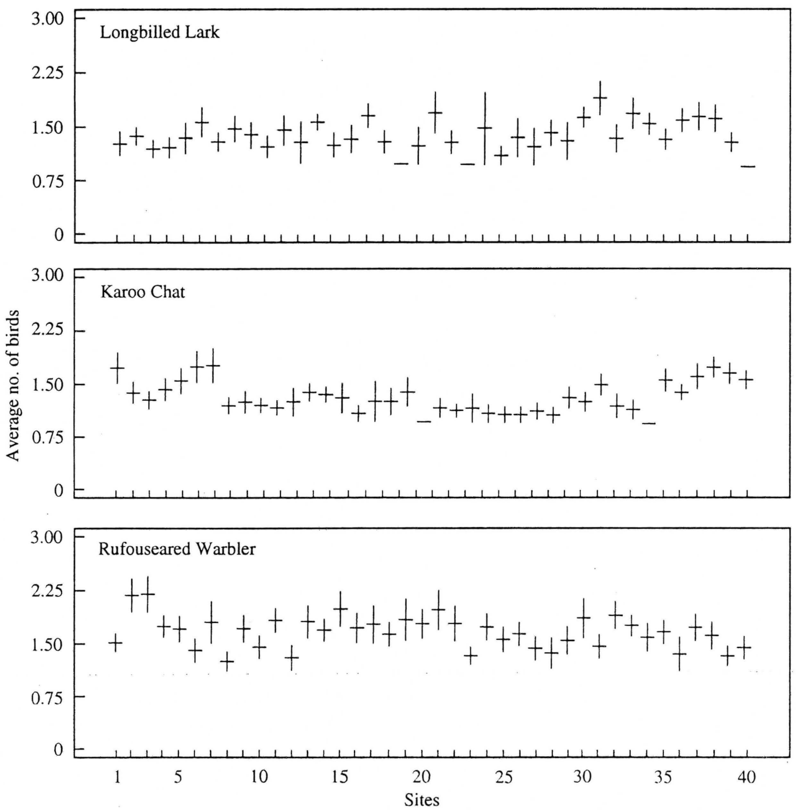

Figure 12. Average (± 1 S.E.) number of selected resident species at each site, all months combined.

Lark-like Bunting) tended to be more abundant at different sites. This implies that there may be competitive exclusion between the two species. Alternatively, there may have been small differences in soil surface characteristics or grass:shrub ratios, or habitat structure between the sites. No evidence was collected to support either of these hypotheses. The two species nested in the same general area during August 1988 so it is unlikely that competitive exclusion, if it exists at all between the species, is constant. The hypothesis that competitive exclusion may partition the habitat in small granivorous birds is supported to some extent by a recent study. The abundances of small granivorous bird species in the Sonoran Desert, south-western U.S.A., were found to be unrelated to food availability (Repasky and Schluter, 1994). These authors concluded that differences in distributions of species in similar habitats were due to interspecific competition, although this was not tested.

It is also of interest that Grey-backed Finchlark and Lark-like Buntings tended to be more abundant (present in larger flocks) during the drier years, a pattern also shown by the canaries. Assuming that the drier years mean less available food, this finding supports Cody (1971), who found that flocks of small granivorous emberizid sparrows

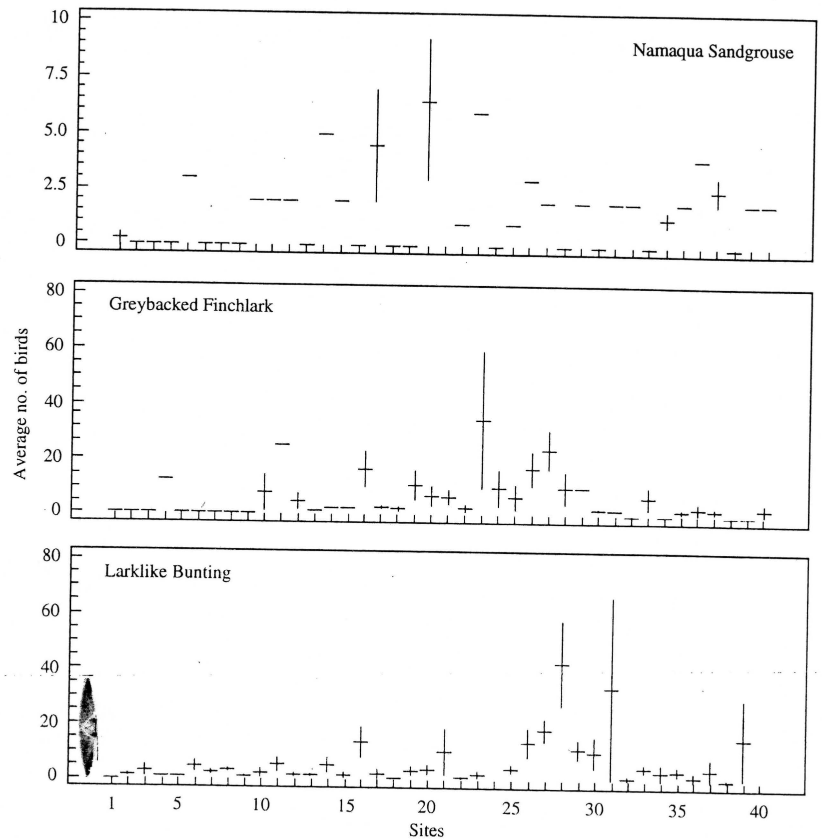

Figure 13. Average (± 1 S.E.) number of selected nomadic species at each site, all months combined.

and fringillid finches in the Mojave Desert, south-western U.S.A., were larger in years of relatively lower food supply. Similarly, Liversidge (1980) found that seed-eating birds increased in numbers in dry periods in the Kalahari Desert.

The results from the present study do not provide the clear evidence of environmental tracking by birds shown in other studies (Pulliam & Parker, 1979; Grant & Grant, 1980; Capurro & Bucher, 1982; Brown *et al.*, 1986; Schluter, 1988; Schluter & Repasky, 1991; Thompson *et al.*, 1991). Nevertheless we provide sufficient evidence to show that avian species richness and abundance in patches in the southern Karoo can vary between years and between sites with similar vegetation, and that movements in nomadic bird species are irregular, both seasonally and annually, and may not necessarily be correlated with local environmental conditions.

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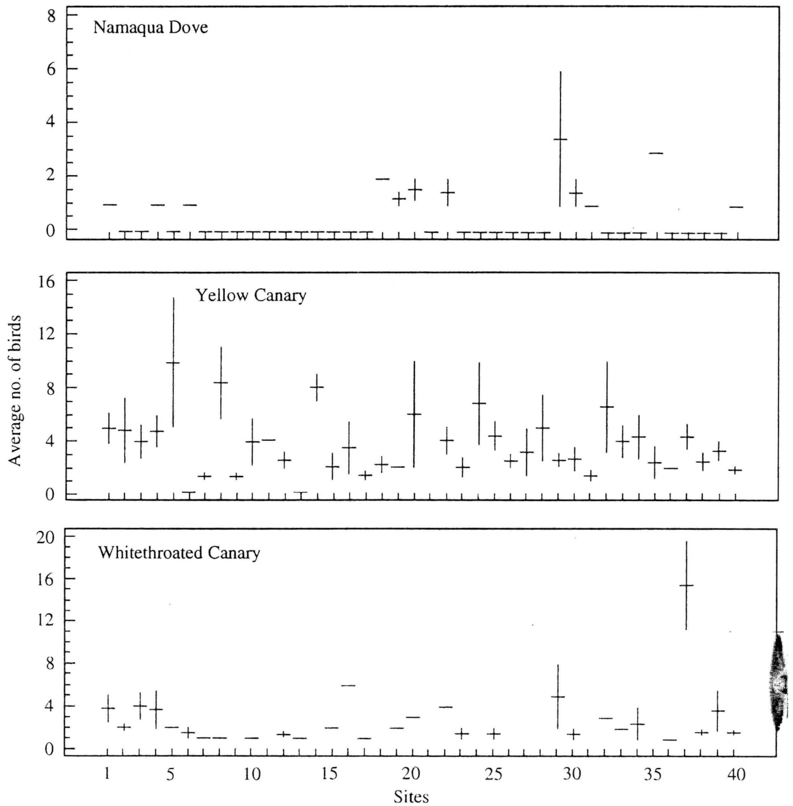

Figure 14. Average (± 1 S.E.) number of selected locally nomadic species at each site, all months combined.

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