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and Southern Hemispheres: a Comparison**

Gordon Lindsay Maclean

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AVIAN ADAPTATIONS TO DESERTS OF THE NORTHERN AND SOUTHERN HEMI-SPHERES: A COMPARISON

G. L. Maclean

Department of Zoology and Entomology, University of Natal, Private Bag X01, Scottsville 3209, South Africa (C. Y. O'Connor Fellow in the School of Environmental Biology, Curtin University, 1996)

Abstract

Ecologically, arid regions can be classified as temperate and hot, and arid or semiarid. The avifaunas of temperate arid and semiarid zones are subjected to seasonally-extreme temperature fluctuations, that necessitate (a) seasonal breeding and (b) a high incidence of migration. Such zones occur at high latitudes and high altitudes. Seasonal breeding is also a feature of birds inhabiting hot hyperarid regions such as the Namib and Atacama Deserts, where environmental cues other than photoperiod are largely absent and therefore irrelevant. Birds of hot deserts, although subject to erratic rainfall regimes, are usually able to capitalise on precipitation as a cue for breeding activity at any time of the year, although retaining an innate response to photoperiod under conditions of abundant food supply. The hot deserts of the northern hemisphere are nevertheless more seasonally variable than those of the southern hemisphere. Northern avifaunas therefore show characteristics that are more similar to those of temperate-desert avifaunas than to those of the southern hemisphere.

Introduction

Major deserts of the world and associated zoogeographical regions are shown in Table 1 and Figure 1. The basic ecophysiology of birds adapted to arid conditions is similar in these areas, the main exception being that the timing and regulation of breeding differ from one arid region to another because of different local environmental pressures (Maclean 1996). Such differences are probably more marked between the deserts of the northern hemisphere and those of the southern. Generally speaking, no matter how severe the aridity, climatic events in the northern deserts are more strictly seasonal than those of the southern. This means that the breeding of northern birds tends to be more seasonally regular than that of birds in the southern hemisphere deserts. There are exceptions to this tendency, however. Wiens (1991) sounds a cautionary note concerning any comparison such as those being made in this paper, to the effect that..."Much of the theory that guides our investigations of communities has been developed with reference to north-temperate situations...and there is a tendency among ecologists to expect it to apply more globally." Ecologists in the southern hemisphere and in the tropics are all too aware of the broadly boreal bias often imposed on ecological interpretations.

Animals in general, and desert animals in particular, usually modify their physiological machinery to cope either with rich episodic resources or with the continuously available low-quality resources that characterise desert ecosystems (Louw 1990). It is difficult to make a distinction between behavioural and physiological adaptations in animals, as is traditionally done, since they may be governed by similar regions of the brain, especially in invertebrates. Louw rightly suggests that such a distinction is

in any case largely semantic..."both physiology and behaviour ultimately become the physics and chemistry of cells." Behavioural adaptations of desert animals are as important for survival as are physiological adaptations, and indeed may be even more important in the absence of special physiological mechanisms. The adaptations of birds, therefore, are likely to be much the same in the different deserts of the world, but differences that exist will be governed by local ecological (mainly climatic) conditions, so it is these that need to be examined most closely when comparing such adaptations.

Table 1: Major deserts of the world and associated zoogeographical regions (mainly after McGinnies 1979).

Afrotropical	Australasian	Neotropical	Nearctic	Palaeartic
Karoo-Kalahari	Gibson	Atacama-Peru	Chihuahuan	Arabia
Namib	Great Sandy	Patagonia	Great Basin	Chang Tang
	Great Victoria	Puna	Mohave	Gobi
	Simpson		Sonoran	Iran
	Sturt			Sahara
				Somalia-Chalbi
				Takla-Makan
				Thar (India)
				Tsaidam
				Turkestan

The purpose of this paper is to present an overview of the movement patterns, dietary categories and factors initiating and regulating breeding in desert birds of the northern and southern hemispheres, emphasising the effects of environmental (extrinsic) factors, while not neglecting what is known about intrinsic physiological reproductive cycles in the birds of these habitats. The only previous comparative study of birds in arid zones of the northern and southern hemispheres has been that of Wiens (1991). Though deserts fall into zones of high atmospheric pressure, and though there may be regular hot and cold temporal patterns, it is not always these regular fluctuations that govern breeding. In most deserts, even the most seasonal in all other respects, the timing of local rain usually has a major effect on the timing of avian breeding. An exception to this generalisation is found, not unexpectedly, under the most arid conditions, where reliance on rainfall would be ecological suicide. Such regions include the fog and rainshadow deserts of the Pacific seaboard of South America and the Atlantic seaboard of Namibia and Angola in southern Africa.

Since there are climatically "temperate" and "hot" desert in both the northern and southern hemispheres, it is necessary to examine their features, in order to determine the different environmental pressures on their organisms, and therefore the adaptive requirements of those organisms for local conditions. It is also necessary to examine the dietary preferences of the birds and the associated movements (migration, nomadism, residency) that affect the timing and duration of breeding activity.

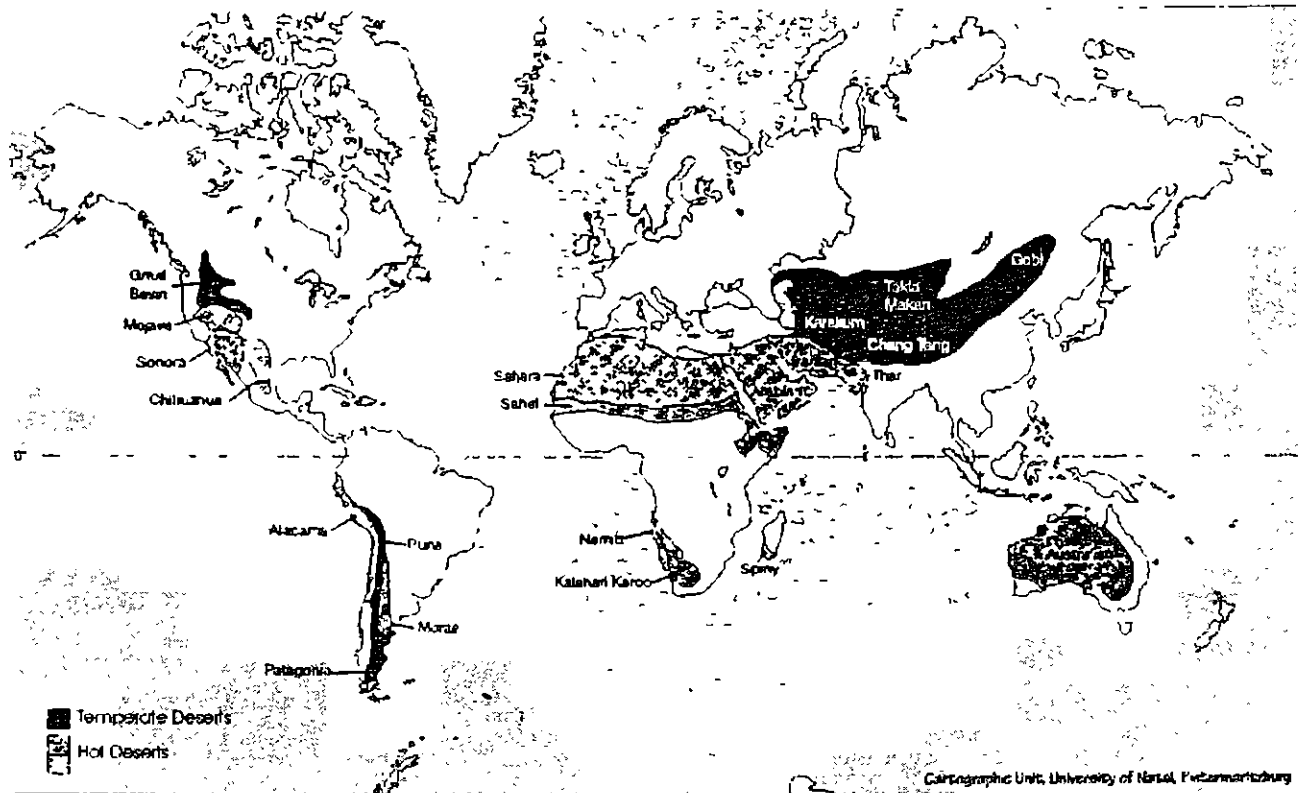


Figure 1: Temperate (“cold”) and hot desert regions of the world, as defined in the text.

The temperate deserts

Much of the Nearctic and Palaearctic arid regions is classed as “temperate desert and semi-desert” (West 1983a; Walter & Box 1983a). The only arid region in the southern hemisphere that falls into this temperate category is the Patagonian Desert of South America (Soriano *et al.* 1983). The remaining northern hemisphere arid regions are classed as “hot deserts” or “arid shrublands” (Evenari 1985).

West (1983b) categorises temperate deserts as those, located between latitudes 28° and 50°, that consistently experience winter temperatures below 0 °C. Snow may accumulate for at least a few days and rarely lies for more than a few months. The vegetation is usually characterised by scattered shrubs with varying amounts of herbaceous plants in between. Of the world’s temperate deserts, only the Patagonian desert has contact with a marine coastline; it is also on average at a lower elevation than the northern hemisphere deserts. It is further unique by being the only arid zone on an east coast, where its aridity is intensified by the cold Falkland Current that inhibits the landward movement of moist air. The Puna is a high, cold, windy semi-desert in the Andes, with a severe climate that undergoes a winter pulse of temperature ranges every 24 hours. Its biota has close evolutionary links with that of Patagonia. Both are “microthermal” deserts. All of these arid regions are bordered at their lower-latitude and lower-altitude edges by hot deserts (Mares *et al.* 1985).

Parts of the Palaearctic arid region are also very high. For instance, the plateau of Tibet and the Pamir have an average elevation of around 4000 m above sea level. Here, the summers are very short and frost occurs throughout the year. About half of Tibet is an extremely arid region called the Chang Tang (“Northern Plain”), an empty, desolate and extremely cold desert of 1,106,000 km², that includes the

Zaidam in its eastern basin (Vaurie 1972). Winter temperatures may fall below -40°C , and summer temperatures seldom exceed 20°C over most of the region, although they may reach 33°C in the Zaidam basin. Even in summer, temperatures may drop below 0°C on any day and snow may fall. Rainfall is restricted to the three months of July-September and does not exceed 250 mm per year. Transitional from this high, cold plateau desert is the Tsaidam ("Salt Marsh") Desert, one of the driest areas, lying in the westernmost Takla Makan, parts of that are below sea level and have extremely hot summers (McGinnies 1979). The Karakum ("Black Sand") Desert of Turkmenistan covers about 366,000 km², of that nearly 70% is rangeland that experiences no snow cover in winter. So the temperate deserts of Asia are quite variable.

The Eurasian arid zone extends from the Aral-Caspian region in the west to Inner Mongolia in the east, and is distinguished from subtropical deserts by its very cold winters that are produced by the East Siberian winter high-pressure system (Walter & Box 1983a). The most westerly parts of this region still experience the remains of precipitation from the Atlantic, especially in winter, becoming drier towards the east. The opposite is true of the most easterly parts: east-moving rainfall occurs in the summer, decreasing westward, so that the central parts of this entire region are the most arid (almost completely rainless in the desert of Takla Makan, on the eastern slopes of the Tien Shan range in the western Chinese province of Sinkiang).

The sheer size of the Eurasian temperate arid regions is reflected by the diversity of habitats within them. The North American arid zone is smaller, but also fairly diverse. All the North American temperate deserts are in the interior of the continent (West 1983a), and are largely rainshadow effects. The Patagonian desert is only about 20% of the size of the North American arid region, and is consequently much more homogeneous. The American and Eurasian deserts are continental, and their aridity is intensified by the rain-shadow effect of the mountain ranges to the east and south of these regions. The aridity of these mountains (orobiomes) is in part a result of their great elevation, resulting in low temperatures.

The faunas of the different zoogeographical regions are taxonomically very different from each other, though their general adaptations to aridity are similar.

The hot deserts

Northern hemisphere

Hot deserts have average temperature maxima above 40°C (usually $45-47^{\circ}\text{C}$), with a mean annual temperature of more than 20°C . Although the Saharan hinterland is hot, especially in summer, nowhere does the average maximum reach 46°C . The hottest parts are in southern Algeria, the absolute maximum ranging from $45-55^{\circ}\text{C}$. The highest maximum temperature on record in any desert was 58°C in the Libyan Desert, but the overall hottest deserts are the Sahel of North Africa and the spiny desert of southwestern Madagascar (Evenari 1985). Indeed, Madagascar is said to have the highest mean maximum of any desert ($19-22^{\circ}\text{C}$) and the smallest temperature difference between the coldest

and hottest months of the year, in part because it is influenced by the warm waters of the Mozambique Current along its western seaboard.

Rainfall in the hot deserts is uncertain. A measure of uncertainty is the variability coefficient, M/m , where M is the maximum annual rainfall and m the minimum annual rainfall. This coefficient ranges in most hot deserts from 6-20, but may be as high as 100 or more. Generally, variability is inversely correlated with the amount of precipitation. The variability coefficient for temperature can be measured in the same way, but it is usually much lower than that for rainfall, e.g., it is only 1.9 in the Negev Desert of Israel.

The more southerly reaches of the northern hemisphere deserts, resulting from high-pressure zones straddling the Tropic of Cancer, include the Mojave, Sonoran and Chihuahuan Deserts of North America, the Sahara and Sahel of North Africa, the Negev and Arabian Deserts of the Middle East, and the Thar Desert of northwestern India. Although the Atacama Desert stretches just north of the equator into Peru and Ecuador, it will be considered under the southern hemisphere deserts, since climatically it has more southern qualities than northern, and also because it is continuous with the rest of the Atacama Desert that extends southward into Chile.

North America

The Mojave Desert is mainly a winter-rainfall region (50-125 mm per year), and grades through the Sonoran Desert to the summer-rainfall of the Chihuahuan Desert in the south. The Sonoran Desert has a bimodal rainfall regime and is the hottest of the three regions. The Chihuahuan Desert experiences relatively minor seasonal changes in climate and is a wintering ground for more northerly bird populations (Raitt & Pimm 1976).

Middle East, Arabia and the Thar Desert

Rainfall in the Middle East occurs under unstable conditions and is "extremely capricious" in both time and space (Orshan 1986). This is typical of desert rainfall the world over: the coefficient of variation is inversely proportional to the amount of rain, being as much as 73% in southern Israel. There is, however, a general trend: light showers fall in early autumn (September-October), followed by heavier showers at the end of October and November and the main rains from late December to February. Rainfall tails off to the middle of May. Dew is also an important form of precipitation, unlike the situation in Australia where the relative humidity is extremely low. Although dew does not affect the moisture content of the soil to any significant extent, it has an important effect on plants and some animals.

Rainfall on the Arabian Peninsula is mainly a winter phenomenon; the months of July to October are rainless, though rain is uncertain at best and droughts are typical. Variability is greatest where the rainfall is least (Abd el Rahman 1986). There is little useful information on the birds of this region, although data provided by Gallagher & Woodcock (1980) for Oman are analysed in Table 2.

Table 2: Main breeding seasons and diets for desert birds of Oman (from Gallagher & Woodcock 1980).

Species	Start of breeding	Main diet
Bartailed Lark <i>Ammomanes cincturus</i>	February	Seeds, insects
Blackcrowned Finchlark <i>Eremopterix nigriceps</i>	February-April	Seeds (?)
Brownnecked Raven <i>Corvus ruficollis</i>	February	Omnivorous
Creamcoloured Courser <i>Cursorius cursor</i>	April (?)	Insects
Crowned Sandgrouse <i>Pterocles coronatus</i>	March-April	Seeds
Desert Lark <i>Ammomanes deserti</i>	January-March	Seeds
Dunn's Lark <i>Eremalauda durni</i>	Unknown	Seeds (?)
Hooded Wheatear <i>Oenanthe monacha</i>	March (?)	Insects
Hoopoe Lark <i>Alaemon alaudipes</i>	February	Seeds, invertebrates
Houbara Bustard <i>Chlamydotis undulata</i>	February	Plant material
House Bunting <i>Emberiza striolata</i>	January	Seeds
Hume's Wheatear <i>Oenanthe alboniger</i>	February	Insects
Mourning Wheatear <i>Oenanthe lugens</i>	February (?)	Insects
Rock Martin <i>Hirundo fuligula</i>	February	Aerial insects
Sand Partridge <i>Ammoperdix heyi</i>	March-April	Leaves, seeds
Scrub Warbler <i>Scotocerca inquieta</i>	March	Insects
Sooty Falcon <i>Falco concolor</i>	July	Small birds
Spotted Sandgrouse <i>Pterocles senegallus</i>	February (?)	Seeds
Trumpeter Finch <i>Bucanetes githagineus</i>	(?)	Seeds
Whitecrowned Wheatear <i>Oenanthe leucopyga</i>	(?)	Insects

The Thar Desert of northwestern India is somewhat unusual when compared to other hot continental deserts in that it has a high relative humidity because of the monsoon circulation of air peculiar to India (Gupta 1986).

North Africa

Most of North Africa is arid, from the Atlantic coast to Egypt and into the Arabian Peninsula, the Thar Desert of northern India and the temperate deserts of central and eastern Asia. The most northerly parts of the African arid region are influenced by the Mediterranean winter-rainfall regime. Rainfall in the most arid parts of the Sahara is negligibly low, but increases northward to about 400 mm at the edge of the arid zone (Le Houérou 1986). The northern parts receive rain from about September to April or May. The more southerly (and more arid) parts can hardly be described as having seasonal precipitation, but there is a trend towards an increasing incidence of rain in the summer under the influence of tropical weather systems. As elsewhere, the variability of rainfall is inversely related to

the amount of rain, ranging from 40% to around 80% from the 400 mm isohyet in the north to the most arid parts in the south (Le Houérou 1986).

Le Houérou (1986) states that... "any particular month in any particular year may be abnormally rainy or absolutely dry, and there is no correlation between consecutive months...; rainfall is totally unpredictable..." A similar pattern of rainfall prevails in Egypt, but the Sudan is largely a summer-rainfall region, becoming increasingly less arid towards the south (Ayyad & Ghabbour 1986). South of the Sahara proper, extending in a belt from the Atlantic coast to the Red Sea, is a region known as the Sahel, that receives between 100 and 500 mm of rain a year, concentrated into a few summer weeks (Monod 1986). Precipitation is irregular.

Southern hemisphere

With the exception of Patagonia and the Andean Puna region, deserts of the southern hemisphere are classifiable as "hot" deserts. They include the Atacama Desert of Peru and Chile, the Monte of Argentina, the Namib, Karoo and Kalahari of southern Africa, the Spiny Desert of Madagascar and the Great Sandy, Great Victoria and Simpson Deserts of Australia.

South America

The arid zone of South America is divisible into four distinct regions, two of them cold (Patagonia and the Puna) and two of them hot (the Monte of Argentina and the Atacama of Chile and Peru). Patagonia and the Puna have already been mentioned.

The Monte Desert is "megathermal", with a sporadic, mainly summer rainfall. The zone has a great latitudinal and altitudinal range, with summer rainfall consequently varying from about 60% of the total rainfall in the north to only 31% in the south (Mares *et al.* 1985).

The latitudinally-longest arid region in the world is the Peru-Chilean region, generally known as the Atacama Desert, stretching from just south of the equator in Ecuador to around 30 °S near Coquimbo in Chile. This arid region is hot only in the coastal lowlands and lower western foothills of the Andes, and in the hyperarid inter-Andean valleys (Rauh 1985). The aridity of the Atacama Desert is ascribable to the cold Humboldt (Peru) Current that flows northward along the Pacific coastline. This cold current also results in the Atacama being a fog desert (the fog is known locally as the *garua* and may penetrate inland from the coast for up to 40 km) with a high relative humidity, especially in winter. The *garua* is absent from about November to April. Above the fog zone, the desert is very dry and may have no vegetation at all.

Australia

The arid zone of Australia may be divided into five "major deserts", though they are continuous with one another (Williams & Calaby 1985): the Great Sandy, Gibson, Great Victoria, Simpson and Sturt deserts. None of these are hyperarid. The difference between humid and arid regions in Australia lies

in the probability of rainfall, rather than in the type of rain, since the belts of high and low pressure do not move north and south or east and west with great precision; nor are the cells of predictable size, pressure, direction and speed (Williams & Calaby 1985). Because of the low relative humidity in Australian deserts, dew, fog and mist are uncommon, except after the rare rains.

Southern Africa

(a) The Namib Desert

Rainfall in the coastal Namib varies between 9-27 mm each year, although the relative humidity is generally high because of frequent fog that flows in over land from the cold Benguela Current on the Atlantic coastline. On average, about 121 foggy days occur per year at Swakopmund, with a winter peak in occurrence equal to a rainfall of about 130 mm a year (Werger 1986). There are therefore only a few hot days in the year, and the region is practically free of frost (Walter 1986). Precipitation is erratic and unpredictable, varying greatly in timing, place and amount. The aridity is intensified over most of the Namib, however, in that most rain falls in summer in the form of thunderstorms, except in the south that has a generally winter rainfall.

(b) The Karoo and the Kalahari

As in the case of the Namib Desert, the Karoo in its southern and westernmost reaches is a winter-rainfall region, but most of the Karoo and all of the Kalahari are primarily summer-rainfall (mainly October-March) regions (Werger 1986). As with any other arid or semiarid zone, however, rainfall is erratic and somewhat unpredictable in time and space. The rain often comes in the form of short thunderstorms. Maximum temperatures exceed 40 °C and have been known to reach 48 °C in the valley of the Orange River. The continental nature of these inland deserts results in nighttime temperatures in winter well below freezing point, though usually not below -10 °C.

(c) Madagascar

The extreme southwestern corner of Madagascar is classed as subarid, while much of the adjacent area is semiarid (Rauh 1986). The subarid region is a rather narrow coastal strip, mostly less than 50 km wide, and has no pronounced rainy season: its annual average of 350 mm is distributed throughout the year. Temperatures may reach 40 °C, but insolation is intense and soils may reach 70 °C. However, the relative humidity is high near the coast, leading to the frequent formation of fog and dew. This is the well known "Spiny Desert" of Madagascar.

Birds of the northern hemisphere temperate deserts

Turkmenistan

The avifauna at the desert research station near Repetek in the Karakum Desert of Turkmenistan, one of the better studied deserts of the northern hemisphere, consists of 25 nesting species, of that 13 (52%) are migratory (Walter & Box 1983b; Table 3). Only 60 species of birds have been identified for the whole of Turkmenistan, an area of 488,100 km². Of the breeding species, 21 (84%) nest in dense stands of Black Saksa'ul (saxaul) *Haloxylon ammodendron* (Chenopodiaceae). The White Saksa'ul

Haloxylon persicum occurs as scattered shrubs in sandy country and is the favoured nesting habitat of the Egyptian Nightjar *Caprimulgus aegyptius* and the Desert Sparrow *Passer simplex*. Both species of saksá'ul are used as nesting habitats by the Streaked Scrub Warbler *Scotocerca inquieta*, Crested Lark *Galerida cristata*, Saxaul Sparrow *Passer ammodendri*, Eurasian Turtle Dove *Streptopelia turtur*, Rufous Scrub Robin *Erythropgia (=Cercotrichas) galactotes* and European Nightjar *Caprimulgus europaeus*. Sandy habitats, whether mobile or stable, are the preferred nesting habitat of Pander's Ground Jay *Podoces panderi* and the Desert Warbler *Sylvia nana*.

Table 3: Dietary and migratory categories of birds for some of the world's deserts. Figures provided denote percentages of total species allocated to each each category, and are based on information taken from references cited in the text. The first nine regions (deserts) mentioned are located in the northern hemisphere, the remaining five in the southern hemisphere. * Dietary subdivision excludes migrants and raptors. † Dietary categories analyzed for breeding species only. ? information not available.

Desert region	Main dietary category				Movement pattern	
	Insectivore	Granivore	Omnivore	Raptor	Migrant	Resident or nomad
Afghanistan and Iran	55	40	-	5	43	57
Blackbrush desert (Nevada)	?	?	?	?	73	27
Oman	35	55	5	5	25	75
Sagebrush (Idaho)	27	20	13	40	?	?
Sahel*	42	35	23	-	40	60
Salt-desert shrub (Utah)	46	28	5	21	62	38
Tibet†	57	29	3	11	53	47
Touran (Iran)	?	?	?	?	65	35
Turkmenistan	?	?	?	?	52	48
Ancón (Ecuador)†	61	27	2	10	62	38
Fowler's Gap (Australia)†	69	15	4	12	13	87
Kalahari (southern Africa)†	58	14	5	23	17	83
Monte (Argentina)	56	21	2	21	?	?
Patagonia (Tierra d' Fuego)†	52	23	0	25	52	48
Means (northern hemisphere)	43	34	8	15	52	48
Means (southern hemisphere)	59	20	3	18	36	64
Means (cold deserts)	47	28	4	21	57	43
Means (hot deserts)	50	23	7	15	36	64
Means (all regions)	50	27	6	17	44	56

Nesting substrates of the abovementioned species are shown in Table 4. From this it is clear that (a) the seasonal nature of the climate makes migration a necessity for many species of birds and (b) there are relatively few species of birds that live and nest on the ground (in contrast to those of deserts of the southern hemisphere, e.g., Patagonia, Kalahari, Australia). After the breeding season, resident insectivores

tivorous species of birds (especially those of the mobile sandy habitats) change their diet to include fruits and seeds of desert plants. This behaviour would obviate the need to migrate.

Table 4: Nesting substrates of birds breeding in stands of *Haloxylon ammodendron* and *H. persicum* at Repetek, Turkmenistan (Walter & Box 1983b; Flint *et al.* 1989).

Species	Nesting substrate
Blackbilled Desert Finch <i>Rhodospiza obsoleta</i>	bush, tree
Booted Warbler <i>Hippolais caligata</i>	bush, ground
Crested Lark <i>Galerida cristata</i>	ground
Desert Sparrow <i>Passer simplex</i>	hole in tree
Desert Warbler <i>Sylvia nana</i>	bush
Egyptian Nightjar <i>Caprimulgus aegyptius</i>	ground
Eurasian Hoopoe <i>Upupa epops</i>	hole, burrow
Eurasian Turtle Dove <i>Streptopelia turtur</i>	tree
European Nightjar <i>Caprimulgus europaeus</i>	ground
Golden Eagle <i>Aquila chrysaetos</i>	tree
Great Grey Shrike <i>Lanius excubitor</i>	tree
Great Tit <i>Parus major</i>	hole in tree
Isabelline Wheatear <i>Oenanthe isabellina</i>	hole, burrow
Lesser Whitethroat <i>Sylvia curruca</i>	tree, bush
Little Owl <i>Athene noctua</i>	hole, burrow
Longlegged Buzzard <i>Buteo rufinus</i>	tree
Northern Raven <i>Corvus corax</i>	tree
Pander's Ground Jay <i>Podoces panderi</i>	bush
Rufous Scrub Warbler <i>Erythropygia galactotes</i>	bush
Saxaul Sparrow <i>Passer ammodendri</i>	tree
Shorttoed Eagle <i>Circaetus gallicus</i>	tree
Subalpine Warbler <i>Sylvia cantillans</i>	bush
Upcher's Warbler <i>Hippolais languida</i>	tree, bush
Whitewinged Woodpecker <i>Dendrocopos leucopterus</i>	hole in tree

Tibet

The Chang Tang has over 150 breeding species of birds, excluding waterbirds (Vaurie 1972). An analysis of these according to diet and movements is shown in Table 3. Most of the species are migratory, while other undertake seasonal changes of habitat and other local movements, especially altitudinal. Unfortunately, Vaurie gives no breeding data, although it is unlikely that the climate would allow of breeding for more than a very short period in summer, say from June to August.

Afghanistan and Iran

A list of the birds of this region, compiled from various sources by Breckle (1983) consists of 40

species. An analysis of the main diets and movements of these species is shown in Table 3. Of the 23 migrants, 15 (37.5%) are fully migratory and eight (20%) are migratory in the northern parts of their range (Flint *et al.* 1989). Similarly, of 158 species of birds recorded in the Touran Biospheric Reserve, Iran, only 35 (22%) were resident (Table 3).

North America

(a) Intermountain Sagebrush Steppe

In the dry Intermountain Sagebrush Steppe of southeastern Idaho, only 15 species of birds have been recorded (West 1983c). Curiously, though it is not listed in his table of species, West mentions elsewhere in his paper that the Sage Grouse *Centrocercus urophasianus*... "reaches its greatest abundance in this type". He adds that... "smaller birds occur in this type with surprising abundance", but that the larger raptors have probably declined as the number of Jackrabbits *Lepus californicus* has fallen. An analysis of the dietary categories of the 15 species appears in Table 3.

(b) Intermountain Salt-desert Shrubland

For sites in Utah in Intermountain Salt-desert Shrubland, West (1983d) lists 53 species of birds. Table 3 gives the dietary subdivisions of these species. The most dominant family in terms of the number of species is the Emberizidae with 12 species, followed by the Accipitridae with six species. Several species are occasional visitors to this ecosystem, and only the Horned Lark... "is ever seen in any abundance". This situation is quite unlike that for most other deserts, where many granivorous species of birds occur in very large numbers, even if only intermittently. Unfortunately, there is no indication of that species are migrants and that are resident, but an analysis from a standard fieldguide (*National Geographic Society field guide to birds of North America*, 1983) shows that at least 33 species (about 62%) are migratory, leaving the region in winter (Table 3).

(c) Colorado Plateau-Mohavian Blackbrush Semidesert

Of the 26 species of birds recorded from this type of arid region in southern Nevada (West 1983e), only eight are breeding migrants (here listed as "summer residents"), but a further seven species are winter visitors from more northern latitudes, so that relatively few species (only about 27%) are resident (Table 3).

Birds of the southern hemisphere temperate deserts

Patagonia

Unfortunately, treatment of the ornithology of the Patagonian arid region by Soriano *et al.* (1983) is brief and superficial. Of the true arid-zone species, it is remarked that... "the greater part of the species are cursorials". These include the Lesser Rhea, two species of tinamou (Tinamidae), plovers, sandpipers and "numerous passeriformes", mainly members of the suboscine families Furnariidae (*Geositta*) and Tyrannidae (*Neoxolmis* and *Muscisaxicola*). Other passerines mentioned are one species of mockingbird (Mimidae) and "several fringillidae". It is also stated that... "birds of prey are plentiful, but none is exclusively Patagonian" (The same could be said of the raptors of most of the world's arid

zones, to which birds of prey appear to be singularly well preadapted). The impression given is that, with the exception of most waterbirds, the Patagonian avifauna is largely resident and terrestrial. There is no substantial information on breeding, but because of the generally low temperatures, breeding is restricted to the summer months (pers. obs.; Humphrey *et al.* 1970), much as in the north-temperate deserts.

An analysis of the information provided by Humphrey *et al.* (1970) on birds of the northern steppe region of the island of Tierra del Fuego, a southward extension of Patagonia, indicates a total of 67 possible breeding species. Their diets and movements are described in Table 3.

Birds of the northern hemisphere hot deserts

North America

Raitt & Pimm (1976) have divided the 98 species of the avifauna of the North American Chihuahuan Desert into seven categories as shown in Table 5. However, the information as presented by them cannot be compared with that from the other desert regions under review, since their categorisations are not along simple dietary lines. They have shown, however, that most of the migrants in the North American Chihuahuan Desert are seedeaters, whereas the breeding residents are mostly insectivorous. During their period of residence, the migrants are nomadic, tending to concentrate in places where it has rained and where seed production is therefore greatest (much as in other deserts). The densities of migrants far exceed those of residents. These deserts are far enough north to have a large population of breeding migrant species from the tropics, yet far enough south to experience an influx of more northerly species during the winter.

Table 5: Number of species per category of avifauna in the Chihuahuan Desert (after Raitt & Pimm 1976).

Category	Number of species
Aquatic species	11
Breeding species	13
Doves and quails	3
Miscellaneous species	12
Nonbreeding insectivorous passerines	25
Nonbreeding seedeaters	21
Raptors	13

Some of the breeding adaptations of two species of Chihuahuan birds have been studied in considerable detail and may be used as an illustration of the flexibility of some desert birds to fluctuating resources. Annual differences in the abundance of Bandwinged Grasshoppers *Trimerotropis*, the major food items of nestling Cactus Wrens *Campylorhynchus brunneicephalus*, are correlated with differ-

ences in the timing of breeding by the wrens, as well as in their clutch size and breeding success (Marr & Raitt 1983). Territories are usually established by the end of April, and egg-laying usually starts about 2 May. In some years, there is a high degree of synchrony of laying (within a week or two), whereas in others laying occurs over a period of up to seven weeks. Laying is initiated by sharp rises in ambient temperatures, but synchrony appears to be a function of relatively poor resources: the wrens start laying as early as possible in order to have an advantage in interspecific competition later in the season.

Clutch size is positively correlated with food supply: the largest clutches are laid when the abundance of grasshoppers is greatest. Breeding success is similarly correlated with food supply. However, in a relatively poor season, broods of three young or fewer survived better than did larger broods. The Cactus Wren does not have a brood-reduction strategy like that of the Roadrunner, but rather adjusts the clutch size to the prevailing food supply.

The Roadrunner exhibits asynchronous hatching of the eggs, so that older nestlings are able to compete more vigorously for food than are the younger siblings. Smaller nestlings that succumb to starvation because of a food shortage are eaten by the parents.

Sahara and the Middle East

With respect to the arid-zone birds of the Middle East, an analysis of breeding information from Paz (1987) shows that the breeding of almost all desert birds in Israel is highly seasonal (Table 6). Only two species appear to be markedly affected in the timing of their breeding by rainfall. Of the White-crowned Black Wheatear *Oenanthe leucopyga*, Paz writes... "Nesting dates vary according to the rate of rainfall....: in years of severe drought, this species will not breed at all, while in normal years breeding takes place between the end of February and early April." The Brown Babbler *Turdoides squamiceps* usually breeds from February to July, but may do so in other months; breeding may be resumed in October if conditions are good, but there will be no breeding at all in drought years, except in pairs living near refuse tips or vegetable gardens where food is plentiful.

Birds breeding on the desert fringe in Iraq have similar seasonal breeding regimes to those in Israel (Marchant 1963). As elsewhere, seedeaters breed later than insectivorous species because the food plants need time in that to set seed after flowering.

Further to the southeast in Oman, Gallagher & Woodcock (1980) have provided some information about breeding and diets of 20 species of birds typical of the arid region (Table 2); the dietary information is summarised in Table 3 for comparison with that from other desert regions. About 75% of the 96 species of breeding birds are resident, the rest being migrants. Most breed in the northern spring and summer, but in years of good rains, breeding may start earlier than usual. Generally, the clutch size is smaller than those for birds in more temperate regions, and the clutch may be reduced in years of poor food supply.

Table 6: Main breeding months for desert birds in Israel (after Paz 1987). * Breeding season given for "normal" year, but variable according to rainfall; see text. † Breeding also in January.

Species	Main breeding months							
	F	M	A	M	J	J	A	S
Bartailed Lark <i>Ammomanes cincturus</i>		+	+					
Blackbellied Sandgrouse <i>Pterocles orientalis</i>							+	
Brown Babbler <i>Turdoides squamicep*</i>	+	+	+	+	+	+		
Brownnecked Raven <i>Corvus ruficollis</i>	+	+						
Cetti's Warbler <i>Cettia cetti</i>				+				
Creamcoloured Courser <i>Cursorius cursor</i>				+	+	+		
Crested Lark <i>Galerida cristata</i>		+	+	+	+			
Crowned Sandgrouse <i>Pterocles coronatus</i>				+	+	+	+	+
Dead Sea Sparrow <i>Passer moabiticus</i>		+	+	+	+	+		
Desert Finch <i>Rhodospiza obsoleta</i>		+	+	+	+			
Desert Lark <i>Ammomanes deserti</i>	+	+	+	+				
Desert Wheatear <i>Oenanthe deserti</i>			+					
Egyptian Nightjar <i>Caprimulgus aegyptius</i>		+	+	+				
Eurasian Stonecurlew <i>Burhinus oedicnemus</i>			+	+	+	+		
Fantailed Raven <i>Corvus rhipidurus</i>		+						
Hooded Wheatear <i>Oenanthe monacha</i>		+	+	+				
Hoopoe Lark <i>Alaemon alaudipes</i>		+	+					
Houbara Bustard <i>Chlamydotis undulata</i>		+	+	+				
House Bunting <i>Emberiza striolata</i>		+	+					
Hume's Tawny Owl <i>Strix butleri</i>				+				
Lesser Shorttoed Lark <i>Calandrella rufescens</i>			+	+	+			
Mourning Wheatear <i>Oenanthe lugens</i>	+	+	+					
Pintailed Sandgrouse <i>Pterocles alchata</i>			+	+	+	+		
Scrub Warbler <i>Scotocerca inquieta†</i>	+							
Shorttoed Lark <i>Calandrella brachydactyla</i>			+	+	+			
Sinai Rosefinch <i>Carpodacus synoicus</i>			+	+				
Spectacled Warbler <i>Sylvia conspicillata</i>		+	+	+	+			
Spotted Sandgrouse <i>Pterocles senegallus</i>		+	+	+	+			
Temminck's Lark <i>Eremophila bilopha</i>			+	+	+			
Tristram's Grackle <i>Onychognathus tristramii</i>			+	+	+			
Trumpeter Finch <i>Bucanetes githagineus</i>								
Whitecrowned Wheatear <i>Oenanthe leucopyga*</i>	+	+	+					

In the Sahara the Houbara Bustard *Chlamydotis undulata* does not breed when the rains are insufficient to result in a good growth of vegetation. The breeding period may last for up to six months, starting in December and continuing to May or June; the usual peak of egg-laying along the northern border of the Sahara is March-April (Heim de Balsac & Mayaud 1962; Etchécopar & Hùe 1967). The

Creamcoloured Courser *Cursorius cursor* also has a fairly extended breeding season, usually starting in March, though sometimes as early as February, and lasting through to the end of June or even later (chicks have been found in August). Such an extended breeding period occurs in other North African birds.

Of the four species of sandgrouse (Blackbellied *Pterocles orientalis*, Pintailed *P. alchata*, Spotted *P. senegallus* and Crowned *P. coronatus*) found in the region covered by Heim de Balsac & Mayaud (1962), all appear to breed seasonally from April to July. The Crowned Sandgrouse may start breeding in March. Only the Spotted and Crowned Sandgrouse are true birds of the desert, the other species being confined to semiarid to mesic habitats.

The desert-dwelling Egyptian Nightjar *Caprimulgus aegyptius* breeds from April to June (Heim de Balsac & Mayaud 1962), that is said to be "early" (Etchécopar & Hüe 1967). The breeding seasons of Saharan larks are shown in Table 7. On the basis of this information, it is again clear how closely tied to spring and summer the breeding seasons of Saharan birds are, in spite of capricious rainfall regimes. The same may be said of other arid-zone specialists, such as the wheatears *Oenanthe*, some warblers, buntings *Emberiza*, and sparrows *Passer*. The desert ravens (Brownnecked *Corvus ruficollis* and Fantailed *C. rhipidurus*) start to breed as early as January, but are still seasonal (Heim de Balsac & Mayaud 1962).

Table 7: The breeding seasons of Saharan desert larks (from Heim de Balsac & Mayaud 1962 and Etchécopar & Hüe 1967). * Varies latitudinally: earlier in south, later in north. † In Darfur, Sudan (Lynes, after Heim de Balsac & Mayaud 1962).

Species	Breeding season
Bartailed Lark <i>Ammomanes cincturus</i>	February-June
Blackcrowned Finchlark <i>Eremopterix nigriceps</i>	January-May*
Crested Lark <i>Galerida cristata</i>	April-June
Desert Lark <i>Ammomanes deserti</i>	January-July (sometimes September-October)*
Dunn's Lark <i>Eremalauda dunnii</i>	February-March†
Dupont's Lark <i>Chersophilus duponti</i>	March-June
Hoopoe Lark <i>Alaemon alaudipes</i>	February-May
Lesser Shorttoed Lark <i>Calandrella rufescens</i>	April-June
Northern Thickbilled Lark <i>Rhamphocorys clotbey</i>	January-May (mainly March-May)
Shorttoed Lark <i>Calandrella brachydactyla</i>	April-June (sometimes March)
Temminck's Lark <i>Eremophila bilopha</i>	February-May

Ayyad & Ghabbour (1986) have confirmed that the desert avifauna of Egypt is largely Palaearctic in its affinities, but claim that "the typical desert species of the Sahara as a whole...are not convincingly either Palaearctic or Ethiopian", indicating that the bird fauna is rather specialised and of mixed origins. The main exception to spring breeding among Saharan birds is that of the Sooty Falcon *Falco*

concolor, that nests in August (the hottest month) to take advantage of the food source provided by the temporary abundance of autumn migrants flying south from Europe.

The Sahel

The affinities of the avifauna of the Sahel, that forms a border between the true desert and the African savannahs, are largely Afrotropical (Monod 1986). However, this avifauna is strongly augmented from August to April by nonbreeding migrants from the Palaearctic. In northern Senegal, for example, of 108 species of birds recorded, 27 (25%) are Palaearctic and 77 (71%) Afrotropical (Morel & Morel 1973). Of these, altogether about 40% are migratory. Only about 15% of all species are therefore breeding migrants from the Afrotropical fauna.

Among the resident species in the study area at Fété-Olé in Senegal, only 15 are truly sedentary. The dietary subdivision of the 55 Afrotropical species, excluding migrants and raptors, is shown in Table 3; the insectivorous species are generally uncommon. Of the 15 sedentary species, seven (47%) are granivorous/frugivorous, six (40%) are omnivorous and only two (13%) are insectivorous. Overall, species that are strictly or partly phytophagous (granivores, frugivores and omnivores) are dominant in the avifauna, with respect to abundance and of residency (Morel & Morel 1973).

In the wet season, the number of species is augmented by migrants, both Afrotropical and Palaearctic, but the density of birds varies little from year to year in spite of variations in the rainfall. In the dry season, however, the density of birds varies according to the amount of rain the previous wet season; species most strongly affected are the granivores, that vary according to the amount of grass cover.

The theoretical number of breeding species, both resident and migratory, at Fété-Olé is 62, but in fact only 22 species appear to have been recorded breeding. These may be divided into six granivores, one frugivore, eight omnivores, six insectivores and one predator. The omnivores include a majority of species that are granivorous outside of the breeding season, indicating the importance of granivory among birds of dry regions. In two successive years of recording nests, 114 nests were found, of that 48% occurred in the wet season, the rest in the dry. Some species nest all year round, so that rainfall does not appear to be an important factor in the timing of breeding.

Bird of the southern hemisphere hot deserts

The Kalahari

Of the 148 species of birds recorded in a study area in the Kalahari sandveld of southern Africa (Maclean 1970a), 57 (38.5%) were resident and 10 (6.8%) were nomadic. Only five species (3.8%) were breeding migrants. The remaining 19 migratory species (12.8% of the total) were non-breeders, all but one from the Palaearctic, and mostly classed as “very rare” in the study area. On the other hand, most of the nomadic species were “common” to “abundant”, all were ground feeders and 80% were largely granivorous. All of the breeding migrants were, by contrast, insectivorous and mostly “very rare”; only one of them was common. The diets of the 57 resident species in the Kalahari study area

are shown in Table 3. The three most abundant species were granivorous.

Most species of birds in the Kalahari breed in response to rainfall (Maclean 1970b, c), except for raptors that are seasonal breeders, and the Doublebanded Courser *Smutsornis africanus* that breeds throughout the year (Maclean 1967). The courser lays a clutch of one egg, but nests three or four times a year, regardless of season or rainfall; the small clutch is undoubtedly an adaptation to an environment with low natural resources.

The Namib

The avifauna of the Namib Desert is, not surprisingly, overwhelmingly Afrotropical in its affinities, with the sole exception of the sandgrouse Pteroclididae, that almost certainly have an ancient Palaearctic origin (Maclean 1984a). Ecologically, the avifauna is divisible into (a) residents and (b) nomads. The residents include the endemic Rüppell's Korhaan *Eupodotis rueppellii*, Dune Lark *Mirafra erythrochlamys*, Gray's Lark *Ammomanes grayi* and Tractrac Chat *Cercomela tractrac*, as well as some specialised subspecies of more widespread birds, such as the Karoo Korhaan *Eupodotis vigorsii*, all of that are confined almost entirely to the "summer-rainfall" part of the Namib and are largely seasonal breeders in summer, regardless of rainfall. The two korhaan species lay clutches of one egg each, probably for the same reasons as the Doublebanded Courser, i.e., to accommodate for an environment with very low productivity.

The Dune Lark has an extended potential breeding season from August to May, but has a definite summer peak in January and February. Gray's Lark is usually a late-summer breeder from March to May, the "summer-autumn rainy season" (Willoughby 1971), but has the capacity to breed opportunistically in response to rain at any time of the year (Maclean 1993). Examination of the gonads showed a fairly short period of reproductive inactivity from August to December, when the gonads were mostly small and nonfunctional, and the birds were undergoing their main annual moult (Willoughby 1971). The occurrence of partly-enlarged testes at any time of the year indicated a potential for tonic gonadotropic activity; hence the ability to breed opportunistically after rain at any time. This is doubtless related to the fact that Gray's Lark inhabits mainly the gravel flats of the more inland parts of the Namib, where rainfall is a more likely, if erratic, event than towards the Atlantic seaboard.

Boyer (1988) states that the Dune Lark's breeding is not dependent on rainfall. It is a bird of the dunefields, that are mainly in the coastal region where fog is regular, but rainfall very rare and therefore not a dependable environmental cue for breeding. Rainfall during a 21-month study by Boyer totalled only 3.6 mm (Boyer 1988).

The distribution of the Tractrac Chat extends eastward beyond the borders of the Namib into the Karoo, but the Namib populations are recognised as forming at least three distinctive subspecies, *Cercomela tractrac albicans*, *C. t. nebulosa* and *C. t. hoeschi*, whose breeding seems to be largely seasonal with a peak in September-October, though said to vary according to rainfall (Maclean 1993).

Australia

An analysis of the diets and movements of the 85 breeding species of birds of the semiarid interior of Australia at Fowler's Gap Research Station in northwestern New South Wales, taken from my own fieldwork, is given in Table 3. The percentages are of the same order of magnitude for each category as those for the Kalahari in southern Africa.

Whether breeding in Australian desert birds is seasonal or opportunistic is largely a matter of distribution and of prevailing climatic conditions, but opportunistic breeding is considerably enhanced in an arid region by early maturation of gonads. This has been shown to be especially evident in the Zebra Finch *Taeniopygia guttata*, the young of that may become sexually mature as early as 10 weeks of age (Sossinka 1975). Budgerigars *Melopsittacus undulatus* are sexually mature at the age of 3.5-4 months, but under captive conditions appear not to show any photoperiodic response, whether under short- or long-day photoperiods (Pohl-Apel & Sossinka 1975). This may appear to be in conflict with Wyndham's (1983) findings of seasonal breeding, but if the timing of breeding is determined by food supply, gonadal responses to photoperiod will be overridden under natural conditions, even if they exist.

Wyndham (1983) has shown a pronounced shift in the breeding season of the Budgerigar from the south to the north of its range: in the south, where the rainfall is largely in winter, the birds are migrants, arriving in spring and breeding and departing again in summer; in the mid-latitudes, the rainfall is largely in summer, so that the Budgerigars are present and breeding during the hot months, mainly in spring in the south and summer in the north; in the most northerly parts of its range where there is a well defined summer wet season, the Budgerigar arrives towards the end of the rains, and breeds mainly in autumn and winter. Populations through the range of the species therefore tend to be more regularly migratory and less nomadic than previously suggested, though there may be local exceptions to these seasonal movements in years of unusually high local rainfall. Wyndham has proposed therefore that movements and breeding are directly controlled by the abundance of food, that is determined in turn by a combination of rainfall and temperature. If food is sufficiently abundant, the birds will settle and breed, provided that suitable nest sites in the form of tree holes are available.

South America

The region of Ancón in southwestern Ecuador has a cool dry season from May to November and a warm wet season from December to May. The dry season results in a harsh and desolate landscape, though the sky is overcast most of the time. The wet season is characterised by rain over several days, interspersed by days or weeks without significant precipitation. Rainfall is highly variable from year to year, ranging from about 25-120 cm. Table 8 presents a record of breeding events in the region for the years 1957 and 1958, correlated with rainfall (Marchant 1959). Even though the number of nests started was closely correlated with rainfall from year to year, the timing of rain in the Ecuadorian semidesert is still confined almost entirely to the period from January to April each year, and most resident species of small land birds started to breed before the rains. Breeding of birds is likewise strictly seasonal, though the initiation of breeding in some species may shift by a few weeks, accord-

ing to the start of the rains. The importance of rain as a stimulus for breeding in some species is shown by the fact that, although some rain may initiate breeding in these species at the start of a breeding season, they will cease to breed if no follow-up showers occur.

Table 8: Mean rainfall (mm) and mean numbers of nests started per month from December 1956 to July 1958 for 41 species of birds at Ancón, Ecuador (after Marchant 1959).

	Months during study period							
	D	J	F	M	A	M	J	J
Nests	7.5	107.0	75.0	98.0	93.0	107.5	3.5	2.0
Rainfall	0.0	7.5	210.9	72.5	36.8	0.0	0.0	0.0

The dietary distribution of the 41 breeding species of birds found nesting at Ancón by Marchant (1959) is shown in Table 3. Eleven of these species are migrants within the tropics, but some may remain in the region in wet years. These species are necessarily seasonal breeders and represent a higher proportion of breeding migrants than occurs in most southern hemisphere deserts. The avifauna is augmented by 38 species of Nearctic migrants each year (Marchant 1958), nearly as many as there are recorded breeding species; this is a very different picture from that of most southern hemisphere deserts. It is significant that none of these migrants are granivorous and many are marine, reflecting the proximity of this arid zone to the sea.

The account by Mares *et al.* (1985) of the Monte Desert of Argentina does not include a full analysis of the avifauna, so that it is difficult to make a sound comparison between it and that of the North American desert avifaunas. However, the species are distributed among the families as shown in Table 9 and their dietary categories in Table 3.

Comparison of avian adaptations to the deserts of the northern and southern hemispheres

Reichman *et al.* (1979) claim that... "most of the birds associated with deserts are insectivorous"; they base their generalisation on a North American situation, but the statement is broadly true of all arid regions (Table 3). It is not clear whether "most of the birds" means most of the species or most of the individuals: this is an important distinction to make, since most of the species may well be insectivorous, but the majority of individuals are probably largely granivorous for most of their lives. From the information given by Maclean (1970c) it is probable that, as in the Kalahari, "most of the birds" means most of the species and not most of the individuals. Although the analyses of some desert avifaunas given in Table 3 may contain information that is not strictly comparable, most of the world's deserts have more insectivorous species than granivorous species. This does not, however, reflect the relative densities of birds in these dietary categories, since granivores are usually numerically far more abundant in deserts than insectivores.

Table 3 also shows that the proportion of migratory species is higher in the cold deserts than in the hot.

This is especially the case if only breeding migrants are considered. The high proportion of migrants in the Ancón region of Ecuador is ascribable to many Nearctic waders along the coast; if these species were excluded from the analysis, the proportions would surely be more similar to those of other hot-desert avifaunas.

Table 9: Species abundance for bird families found in the Monte Desert of Argentina (after Mares *et al.* 1985).

Family	Number of species
Accipitridae	3
Apodidae	1
Caprimulgidae	2
Cariamidae	1
Cathartidae	2
Columbidae	3
Dendrocolaptidae	2
Emberizidae	6
Falconidae	4
Furnariidae	8
Hirudinidae	1
Icteridae	3
Mimidae	2
Picidae	3
Psittacidae	2
Rheidae	1
Rhinocryptidae	2
Strigidae	4
Thraupidae	1
Tinamidae	1
Trochilidae	1
Tyrannidae	7
Tytonidae	1

The coastal positions of the Atacama and Namib Deserts and their extreme aridity have allowed the evolution of interestingly parallel breeding strategies of two marine birds, the Grey Gull *Larus modestus* of the Atacama (Howell *et al.* 1974) and the Damara Tern *Sterna balaenarum* of the Namib (Frost & Shaughnessy 1976). No northern hemisphere desert has this unique combination of features, and therefore no equivalent avian breeding strategy. Both the gull and the tern capitalise on the richly produc-

tive waters of the cold ocean currents (Humboldt and Benguela, respectively) for their food supply and on the relatively predator-free desert floor for their breeding habitat.

The Damara Tern nests from October to June in loose colonies on the open desert floor up to 8 km from the coast, with a peak of breeding activity in January (midsummer) (Simmons & Braine 1994). A six-year study gave a hatching success of up to 82% (mean 72%), most of the losses apparently being ascribable to predation by Blackbacked Jackals *Canis mesomelas* (17%) and Pied Crows *Corvus albus* (11%). Some predation by Brown Hyenas *Hyaena brunnea* may have occurred at some colonies, but could not be quantified.

The Grey Gull is a common species of the Pacific coast of South America, yet the only known nesting sites are in the hyperarid deserts of the interior of northern Chile, where colonies of thousands of birds nest on the desert floor about 30 km from the coast (Howell *et al.* 1974). The chicks are fed mainly at night, but both adults and chicks can withstand the intense heat by using evaporative cooling mechanisms, mainly panting. Even unshaded chicks can usually survive if a breeze is blowing. Predators are almost entirely absent from the nesting areas, though chick mortality is high, apparently as a result of overheating in still air and of starvation.

Williams & Calaby (1985) have suggested that the great mobility and the relatively high body temperature of birds confer on them... "considerable advantages... for life in deserts". While this is certainly true, other adaptations operate synergistically to enhance their survival in arid zones, some of that are nasal salt glands, tonic gonadotropic activity and crepuscular or nocturnal activity patterns. Salt glands, present only in some nonpasserines, allow birds to excrete excess salt taken in with the cellular fluids of plants and animals that they eat. Tonic gonadotropic activity allows birds to breed within a very short time after rain, and is especially prevalent in the arid regions of Africa and Australia, the northern hemisphere deserts being more strictly seasonal and their avian inhabitants therefore less flexible. Nocturnality is a strategy that avoids the build-up of excess body heat during daytime activity when the ambient temperatures are high.

Maclean (1984b) has shown that ground-dwelling birds predominate numerically in the Kalahari sandveld, though they consist of only 12 species (21.1% of the total). These include mainly plovers, coursers, sandgrouse and larks. Most of the arboreal species are also ground feeders (30 species, or 52.6% of the total). Only 15 species (26.3%) are strictly arboreal. Ground feeders predominate also in the Sonoran Desert, whereas arboreal species predominate in the Monte of Argentina and the arid zone of Western Australia (Maclean 1996). These situations depend on the relative abundance of trees in the regions concerned.

However, as Williams & Calaby (1985) point out, these adaptations are flexible, so that birds may revert to a seasonal breeding pattern when, in a very wet year, rainfall is no longer a limiting factor, as shown by Maclean (1976a). Nevertheless, the assertion by Williams & Calaby (1985) that only sea-

sonal breeding is successful is probably largely untrue, even of Australian desert birds. It is certainly untrue of southern African desert birds, that have been shown to have their highest breeding success during winter, after good autumn rains in the Kalahari sandveld, mainly because of reduced numbers of snakes (Maclean 1970a, b; 1973a).

With regard to breeding, Riechert (1979) writes..."The timing of reproduction to fit local rainfall patterns appears to be important in a wide range of taxa. Peaks in reproductive activity are often associated with rainy periods." If the rains coincide with a summer breeding season, it may be difficult to decide without adequate experimentation whether birds are responding to rainfall or to photoperiodic phenomena, or even if both are necessary. For instance, some species of birds in the Sonoran Desert nest just before the rains, making best use of the limited food supply at the time, but their young emerge from the nest at a time when the rains result in a greatly augmented food supply. Similar patterns are found in Ecuador (Marchant 1959), where some birds build nests and then wait until the rains before egg-laying. Some Sonoran birds may make a second attempt at breeding after the summer rains within a given season only if the earlier attempt failed, though a few exhibit a definite bimodality in their nesting. The American Mourning Dove *Zenaidura macroura*, a seasonal breeder elsewhere, is a year-round breeder in the Mojave Desert, that is much the same situation prevailing for doves in the southern hemisphere deserts.

Wiens (1991) has compared the ecology of the avifaunas of shrub-deserts in the Great Basin of North America (Oregon and Nevada) and the arid interior of Australia (northwestern New South Wales). Study sites on the two continents were chosen for their almost indistinguishable plant-structural features: shrubs were woody, 30-100 cm tall, more or less leafy throughout the year, with sparse grass between them. The assemblages of breeding birds contained the same number of species per unit area at each site, but the mean density of birds in Australia was about half that in North America. In spite of some apparent ecological convergence, there was little matching of the two sites in terms of ecology and life history: the Australian birds were characterised by longer breeding periods with more breeding attempts per period, greater social aggregation during breeding (often feeding in flocks) and a much lower incidence of true migration, all being sedentary or nomadic at most. The North American species were all migratory. The Australian species showed a greater tendency toward the building of domed nests, rather than open cups.

Australian species tend to be more granivorous and have a significantly greater mean body mass than those in North America, but if the density of species per unit area is taken into account, there is no difference in the biomass of birds per unit area. This means that there are markedly higher densities of breeding species in North America than in Australia.

Many Australian arid-zone birds breed opportunistically after rain, but such an ecological pattern appears to be superimposed on an innate response to seasonal effects (Maclean 1976a). Winter breeding appears to be the rule for the Inland (Australian) Dotterel *Peltohyas australis* (Maclean 1976b), a

possible mechanism for avoidance of extreme heat in its exposed nesting sites during the summer. The same might well be the case for the Namaqua Sandgrouse *Pterocles namaqua* in the Namib Desert (Dixon & Louw 1978), as well as for this and other sandgrouse species in the Kalahari Desert (Maclean 1976c). A review of the earlier literature on the Inland Dotterel (Maclean 1973b) has produced somewhat ambiguous evidence with regard to the breeding season, but more recent information goes some way towards confirming a breeding season that extends from April to October (autumn to spring), regardless of rainfall, though the effects of local rain on the breeding of this species need to be closely examined.

Breeding during the winter in the North American deserts is not possible because of the extremely low environmental temperatures, even if rainfall were a positive factor, whereas birds can breed throughout the winter in Australia (and in southern Africa) if other factors are equal. The greater topographical relief of the North American desert means that favourable habitat is available only in spring and summer, conditions favouring migratory species only. It is these major topographical and climatic differences between the two continental arid zones that obviate close convergence between the ecologies of the respective avifaunas.

On the other hand, the avifaunas of these two deserts are similar with regard to mean clutch size, incidence of polygyny, height of nests above ground, size of territory and general diet. Differences in the species of plants and their communities are very marked between the two sites, even though both sites are dominated by species of *Atriplex* (Chenopodiaceae). The long-term mean precipitation, though similar in average annual amount at the two sites (150-290 mm in North America, 125-260 mm in Australia), is far more variable, both monthly and annually, in Australia than in North America: Australia is subject to widespread and prolonged droughts that, along with the resulting impoverishment of the soil, results in overall lower and more erratic primary and secondary productivity. Prolonged droughts in the North American Great Basin are local rather than regional, and therefore have relatively little overall effect on an analysis of avifaunal strategies. The much greater extent of the Australian arid zone (3-4 times greater than the North American) also tends to make ecological differences less local and more widespread. The Australian arid region is generally warmer than the North American, rarely experiencing frost in winter. Climates and resource levels differ substantially between the two continents and the avifaunas are phylogenetically divergent, hence the major differences in avian ecology that are apparent between the sites.

Overall, Wiens (1991) has concluded that... "the differences between these avifaunas are much more impressive than are the similarities." The only family (under the older, more conservative systematic arrangement) common to both the Australian and the North American desert avifaunas studied is the Corvidae. Differences in their ecologies might be explained by differences in their phylogenies, but the data required to test such a suggestion are unavailable.

The kind of comparison indicated above shows the differences between breeding regimes in the north-

ern and southern deserts even more strikingly when made within a single family, the sandgrouse Pteroclididae. I summed this up (Maclean 1976c) in the following way: (a) sandgrouse in the Eurasian arid regions breed seasonally in spring and summer; (b) in the Sahara they tend to be more rainfall-dependent, but since rainfall there is seasonal the sandgrouse tend also to be seasonal breeders; (c) sandgrouse in southern Africa breed at almost any time of the year, but show a distinct winter peak, probably because seeds are most abundant then, since rainfall, though unpredictable, is mainly a summer phenomenon; (d) sandgrouse breeding in mesic regions breed seasonally. The winter breeding peaks in southern Africa tend to be more pronounced after good summer or autumn rains, even though Dixon & Louw (1978) suggest that neither the abundance of food nor rainfall appear to be important in the timing of breeding of the Namaqua Sandgrouse. This may seem to make good ecological sense in a region of such low rainfall, but sandgrouse are highly nomadic and can capitalise on locally abundant food resulting from localised rainfall. What needs to be determined in this interesting family is the degree of tonic gonadotropic activity, if any, in the more arid-adapted species.

The "integrated view" of Shmida *et al.* (1986) distinguished between adaptations that utilise poor resources and those that utilise episodically rich resources. The former set of adaptations include high physiological tolerance to drought and extremes of temperature, efficient use of existing resources, a low turnover and increased longevity of individual organisms. These adaptations are found especially well developed in plants. The second set of adaptations includes the rapid capture and use of the resources, rapid transition between inactive and active phases of the life cycle or a rapid change in behaviour in response to the sudden availability of an abundant resource. Avian examples are not given, but they can be found quite easily by an examination of those species of birds endemic to the extreme deserts such as the Namib (e.g., Rüppell's Korhaan, Gray's Lark, Tractrac Chat) that use poor resources and are generally fairly thinly but evenly dispersed over the habitat, as opposed to the nomadic or unevenly dispersed birds of the semiarid deserts (larks, the Sociable Weaver) that capitalise on locally rich resources as they become available.

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