Introduction

There are two basic strategies for coping with life in the desert: (1) to be resident and sedentary and by behavioural or physiological tactics able to withstand extremes of heat and cold, lack of water and fluctuations in the availability of food and plant cover, or (2) to be a migrant, and to opportunistically or seasonally move to where these resources are available. For at least one group of animals, the avifauna, both strategies have their advantages and disadvantages (Andersson 1980). For sedentary, resident species the advantages are an intimate knowledge of the patch in which they live, and for some a permanent home, but the quality of life in the patch is variable, and there is no escape from stochastic weather events that may temporarily transform the patch into a place where making a living becomes very hard indeed. For species that move, the advantages are to be able to find a patch where resources are at least in reasonable supply, even though there are associated costs – the energetic costs of moving and maintaining water balance (Maclean 1996), the difficulties of finding patches that offer such resources, increased competition at the patches and the lack of a permanent territory and/or pair bond. For those species that move, the benefits must outweigh the costs (Lack 1954). Sinclair (1984) noted (in summarizing results from Elgood et al. 1973) that very few forest bird species migrate, and interpreted this as indicating that the cost of moving from a relatively benign environment is greater than the difficulties of remaining in it through the mild dry season.

Animals that move from place to place are not restricted to deserts. In temperate regions, hard winters with concomitant food shortages precipitate regular seasonal movements. Local populations may build up to such an extent that individuals become resource limited so that part of the population, at least, is forced to move. Predictable, seasonal movements (migration) and directional one-way movements (emigration and immigration) (Sinclair 1984) are features of animal communities living in environments where resources are abundant during part of the year, and hard to find at other times of the year. Another category of movements, undirected dispersal (Greenwood 1984), usually refers to one-way movements from high-resource areas, where survival and reproduction may be relatively high.

Dispersal is considered to be an adaptation to avoid inbreeding and to reduce competition between relatives (Greenwood 1984) and typically occurs in seasonally high-resource areas like Europe (Greenwood et al. 1978), and seldom in patchy resource areas like the deserts. Deserts (Tables 1.1, 1.2), in the broadest sense, with low and unpredictable rainfall, high coefficients of variation in annual rainfall (Le Houérou et al. 1988), low productivity and patchiness in resources, sparse vegetation, and extremes of heat and cold, have promoted yet another category of movements in animals.

Nomadism, in which the movements are irregular and where destinations may differ from year to year (although both timing and destination may be predictable in the short term), is a form of migration (Kennedy 1985) and an adaptation to use resources that are patchy in space and time. Migrants overfly resources in order to reach a specific destination; nomads may not (Dingle 1996). All members of a nomadic species may leave an area and move together to another patch, so that competition between individuals is not necessarily reduced and inbreeding not necessarily avoided. Depending on environmental conditions, nomadic species may return repeatedly to the same areas, not necessarily at the same times of the year, or they may visit the same areas at the same times of the year, or there may be intervals of several years between visits to certain areas. Nomadic avifaunas are characterized by marked and dramatic increases in the number of birds suddenly appearing in habitats where rain has recently fallen (e.g. Maclean 1970a) or, conversely, "at the height of one of the country's worst droughts" in the Eastern Cape Province, South Africa (e.g. Skead 1995), driven, no doubt, by even less productive environments elsewhere.

Most forms of migration are particularly well developed in birds, and the movements of birds and their seasonal patterns of movements across and between continents and from lowlands to highlands, or the reverse, have

Table 1.1. Temperate deserts and semi-deserts (based on West 1983a, b; Walter and Box 1983; Shmida 1985). These are all "cold" deserts (minimum winter temperatures significantly below 0 °C)

Continent, subdivision [grouping]
Eurasia
Kazakho-Dzungarian deserts (Karakum, Turkestan) and semi-deserts [Cold Asian]
Central Asian deserts (Gobi, Takla Makan) and semi-deserts [Cold Asian]
North America
Great Salt Lake desert and Great Basin-Colorado Plateau [Great Basin Desert]
South America
Patagonian and Puna semi-deserts [Cold South American]

Table 1.2. Hot deserts and arid and semi-arid shrublands (based on Evenari 1985). These are all "warm" deserts (minimum winter temperatures above or about 0 °C)

Continent, subdivision [grouping]
Asia
Arabian, Iranian, Thar and other Indian deserts [Warm Asian]
Africa
North Africa (Egyptian, Sahara and Somalian deserts) [Sahara Desert] and broad belt of arid savanna along the southern edge of the Sahara [Sahel]
Southern Africa (Namib desert and Richtersveld), arid savanna (Kalahari Desert) and arid to semi-arid shrublands (Nama- and Succulent-Karoo) [Southern African]
Madagascar
Southwestern corner [Madagascar]
Australia
Gibson, Little and Great Sandy, Great Victorian, Simpson, Sturt and Tanami deserts Arid to semi-arid savanna and shrublands [Australian]
North America
Chihuahuan, Mohave and Sonoran deserts [Warm North American]
South America
Atacama, Monte and Peruvian deserts [Warm South American]

been of interest to biologists for a long time (Moreau 1972; Keast and Morton 1980; Curry-Lindahl 1981; Kennedy 1985; Alerstam 1990; Berthold 1991; Dingle 1996). Birds, with their mobility and the speed at which they can travel, have developed migration systems of one form or another that enable them to enjoy the best of all possible worlds. This mobility, and the ability to locate sheltered sites, or higher resource patches in landscapes, or to escape from areas that are drying out and becoming unproductive has enabled birds to live in some of the harshest environments on earth, including the southern ice-cap (Ryan and Watkins 1989) and in all of the world's oldest and driest deserts (Serventy 1971; Willoughby 1971; Casselton 1984; Maclean 1996). Much of the earlier literature on birds in deserts and semi-arid shrublands attempts to place movements by birds into a migration framework (e.g. Thomson 1964), and there was little recognition of nomadic movements by terrestrial birds prior to Keast (1959), Immelmann (1963), Serventy (1971) and Rowley (1974). It is worth noting that all these ornithologists worked in arid Australia, where the proportion of nomadic bird species is significantly higher than in any other arid region (see Chap. 3). Even fairly recent discussions of desert birds (e.g. Cowan 1990) divide the avifauna of the Gulf of Aden into "residents, wintering species and visitors on migration", with no mention of nomads, although several of the species listed are nomads in the accepted sense.

This book explores movements in the avifauna of arid regions of the world and the advantages and disadvantages of a migratory or nomadic lifestyle in desert environments. Not all birds that live in deserts need to move far in order to survive. However, for many bird species, movements between habitats or across landscapes to find patches of resources is essential for their continued existence. Rowley (1974) pointed out that nomadism and movements in birds in desert environments are adaptations to the variability rather than the severity of the desert environment. For the purposes of this review, "desert" has been interpreted in the broadest possible sense, and includes all areas with mean annual precipitation below 250 mm. The semi-arid and arid shrublands, and the arid savannas of Africa and Australia with mean annual rainfalls below 500 mm (collectively referred to as "semi-deserts" in this review) have also been included. Boundaries between deserts and semi-deserts, or between hyper-arid (with mean annual rainfall less than 100 mm) and arid (with mean annual rainfall 100–250 mm), and between arid and semi-arid areas (<500 mm) are generally not seen as clear edges by many birds. This is most marked in high rainfall years, when birds may penetrate deep into desert habitats, or in low rainfall years, when "desert" birds may temporarily move into adjacent semi-desert habitat ("drought-driven movements"; Moreau 1966, p. 231). The focus in this book is on the dryland avifaunas, although the nomadic bird species that are

Fig. 1.1. Ephemeral wetland near Brandvlei, Karoo, South Africa, providing breeding habitat for Black-winged Stilts *Himatopus himantopus* and Pied Avocets *Recurvirostra avosetta*

dependent on water are briefly discussed. Ephemeral water bodies (Fig. 1.1) are a feature of desert environments, and birds that occur in deserts and are dependent on water accumulating in lakes and ponds for food and nest sites are obligate nomads, particularly those bird species, such as flamingos, avocets and stilts, feeding on ostracods, cladocerans and brine shrimps. One of the most spectacular responses to unpredictable rainfall events in arid regions by one of these species is shown by the Banded Stilt *Cladorhynchus leucocephalus* in arid Australia, when the birds may appear and breed in very large colonies at sites that may have been dry for decades (Ross 1931; Robinson and Minton 1989; Dingle 1996).

1.1 Arid and Semi-Arid Regions

The true deserts of the world are the Sahara, the Australian, the Arabian, the Turkestan, Takla Makan, Gobi, Atacama and the Namib. Semi-arid and arid shrublands and arid savannas of the world include the Asian shrub steppes, Australian mulga and other dry woodlands, spinifex grasslands and shrublands, the North African dry shrublands and savannas, arid savannas of the Kalahari Desert, arid and semi-arid dwarf shrublands of the Richtersveld and the Karoo *sensu lato* of southern Africa, the southwestern corner of Madagascar, the Great Basin shrublands (including the Great Salt Lake Desert), the Mohave, Sonoran and Chihuahuan Deserts of North America, and the Peruvian-Chilean, Patagonian and Monte Deserts, and arid Puna of South America. The deserts and semi-deserts of the world have been adequately described in numerous reference works, of which the three volumes of "*Ecosystems of the World – Temperate Deserts and Semideserts* (West 1983) and *Hot Deserts and Arid Shrublands* (Volumes 12A and 12B) (Evenari et al. 1985) give a most comprehensive picture of ages, climate, landforms and vegetation (but very little on avifaunas). The major deserts and arid and semi-arid shrublands in the broad grouping used in this book are listed in Tables 1.1 and 1.2.

1.2 The Avifauna of Deserts and Semi-Deserts

The species richness, and the number of birds confined to deserts and semi-deserts (collectively discussed as "deserts" or "arid zones" in this review) are low compared to more mesic areas (Wiens 1991a; Maclean 1996). With the exception of a few species, most of which occur in African, Asian and Aus-

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