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Boom and bust (or not?) among birds in an Australian semi-desert

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ABSTRACT

Australian semi-deserts and their birdlife have been characterised as 'boom and bust' systems with nomadism and seasonal flexibility in the timing of breeding features of the avifauna. However, at least some components of the avifauna persist through dry periods, and the nature of population fluctuations is poorly documented. We examine temporal patterns of bird abundance and community structure with an analysis of six years of annual counts of birds at 66 sites in Newhaven Wildlife Sanctuary spanning a cycle of dry–wet–dry years. Community metrics dichotomised sharply between years with higher and low rainfall in the prior 12 months ('wet' and 'dry' years). Bird abundance was nearly quadruple in wet compared to dry years, and site species richness double, this increase being initially driven by immigration. However, 28 of 48 common species fluctuated little. Our results are consistent with the 'interrupted stasus' model of desert systems in which the avifauna 'boomed' following heavy rainfall but reverted to its prior state when dry conditions re-established. However, as a characterisation 'boom and bust' does not reflect the persistence of the majority of common bird species, nor the ability of these ecosystems to support life through dry periods.

1. Introduction

Most birds live for several to many years and are thus exposed to annual variation in key environmental drivers. Responses to annual cycles of temperature, day length and rainfall may include relatively-fixed annual cycles of seasonal breeding, moult and migration. However, in arid and semi-arid regions, birds may also be exposed to infrequent and unpredictable rainfall events that transform ecosystems and do much to drive their productivity, and such events may be interspersed between multi-year droughts. These events may be interpreted as interruptions to an arid stasus (Dean et al., 2009), and thus as disturbances which can be analysed quantitatively in terms of initial ecosystem properties, environmental drivers of change, and the physical and biological mechanisms of that change (Peters et al., 2011). The predictability of resources in time and space has major implications for the evolution of life histories (Stearns, 1976) and the structure of faunal assemblages (Cheke and Tratalos, 2007; Dean et al., 2009; Albright et al., 2010; Ford, 2013). Here we investigate the response of a bird assemblage to a sequence of ecosystem-transforming rainfall events, seeking to identify the extent and nature of stability and instability in the bird assemblage of a semi-arid environment using an extensive set of counts conducted annually for six years.

With high interannual variation in rainfall and consequent fluctuations in surface water and soil moisture, central Australia's vast semi-arid zone presents many challenges for plant and animal life, as do similarly unpredictable semi-deserts and deserts elsewhere (Holmgren et al., 2006). Emphasizing among-year variation in rainfall, corresponding fluctuations in primary productivity and wildlife populations, and the prevalence of ecological opportunism in the flora and fauna, some have characterised the region's ecosystems (Stafford Smith and Morton, 1990; Morton et al., 2011) and wildlife (Robin et al., 2009; Dickman et al., 2011; Pavey et al., 2014) as being 'boom and bust' in nature. Others have argued that predictable seasonal elements make a significant contribution to the ecology of the region, generating reliable phenologies and maintaining biological activity even under drought conditions (Davies 1976a,b; Walker et al., 1996). These elements include

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temperature, day length, seasonality of rainfall, localised run-off even in dry years, and the phenologies arising from the prevalence of perennial life forms such as trees, shrubs and hummock- and tussock-grasses. Potential reconciliation of these counterpoints was provided by a study of plant growth in Australia's Simpson Desert. Nano and Pavey (2013) found evidence of: a. rain-driven resource pulses particularly among grasses, forbs and the flowering of some woody plants; b. pronounced seasonality in the growth of plant species; c. differential responses to rainfall and seasonality of plant growth forms (grasses, forbs, woody plants); d. differential impacts of soil texture on plant responses; and e. run-off–run-on effects. Reynolds et al. (2004) identified parallel levels of complexity in plant functional responses to rainfall in North American semi-deserts.

The response of land birds to resource fluctuations provides further illumination of these ecological themes of predictability and unpredictability. Bird assemblages at any given location or district in central Australia and other arid regions can be highly unstable over time, varying both numerically and compositionally in response to rain (Marone, 1992; Paltridge and Southgate, 2001; Burbidge and Fuller, 2007; Tischler et al., 2013). Two mechanisms underlie these fluctuations: nomadism (Davies, 1984; Dean, 2004) and changes to survival and recruitment (Dean et al., 2009). Rather less attention has been paid to the existence and nature of relatively-stable components of these bird assemblages. Sedentary species may be predominantly generalists, insectivores or carnivores, whereas nomads are mostly granivores or nectarivores but can also be insectivores (Paltridge and Southgate, 2001; Burbidge and Fuller, 2007; Tischler et al., 2013). The abundance of sedentary species may decline during prolonged drought (Burbidge and Fuller, 2007).

Nomadism comprises irregular resource-driven movements at regional and sub-continental scales. A variant, seasonal migration combined with great interannual resource-driven variation in settlement sites has been termed 'nomadic migration' (Cornelius and Hahn, 2012). Some waterbirds detect and respond promptly to distant ('over the horizon') rainfall events (Roshier et al., 2008; Pedler et al., 2014; Henry et al., 2016), but it is less clear whether land birds respond with awareness that favourable conditions exist elsewhere or because conditions are no longer favourable at their initial site, or some combination thereof. Because rainfall in central Australia has an underlying seasonality, falling predominantly in summer in the north and in winter in the south, some nomadism appears to have a strong migratory (north-south) element to it (Ford, 1978; Wyndham, 1983). This raises the possibility of pre-emptive (evolutionary) adaptation and pre-migratory fattening to support long-distance flight, the latter demonstrated in nomadic migrant Red Crossbills (*Loxia curvirostra*) (Cornelius and Hahn, 2012). However, the Budgerigar (*Melopsittacus undulatus*), a nomadic migrant of Australian deserts, does not deposit fat and migrates in a series of short steps (Wyndham, 1980). Prompt movement in response to distant rains precludes pre-migratory fattening, as perhaps also does movement driven by local exhaustion of food supplies.

Fluctuations in desert bird populations may be driven by reproduction of both nomads and residents, with nest density, clutch size, unseasonal breeding and increased breeding success contributing to this (Morrison and Bolger, 2002; Dean et al., 2009). However, the reproductive response to rainfall of one Australian desert bird (Zebra Finch, *Taniopygia guttata*; resident or local nomad) is variable (Zann et al., 1995).

Although birds display a variety of behavioural and physiological adaptations to the challenges of living in deserts including nomadism and reductions in basal metabolism and cutaneous water loss (reviewed by Dean and Williams, 2004), little is known about ecological differences between nomads and residents of these regions. Theoretically, nomadism (*cf* residence) is expected to be favoured as a 'strategy' to optimise fitness when the interval between major rainfall events is long, and to be associated with larger clutches, high juvenile survival and low adult survival (Andersson, 1980) but, like many studies, evolution and environment are confounded in this study because nomadic *cf* resident congeners tend strongly to separate on environment. Larger clutches might also be anticipated in desert residents than residents of regions with higher and more regular rainfall. Contrarily, many birds of the central Australian semi-deserts have small clutch sizes (e.g. two is common) and fairly slow breeding responses, and these seems characteristic of both nomads and residents (Kikkawa, 1974; Wiens, 1991).

The long term and sub-continental scale of the phenomenon of fluctuating bird populations in Australia's arid zone poses a challenge for studies of it. We here provide count data that spans a cycle of dry-wet-dry conditions (six years of annual counts), and is of unusually large geographic extent: 66 sites spread across 12 vegetation types fully sampling a 261,000-ha reserve – Newhaven Wildlife Sanctuary in the Great Sandy Desert of central Australia. We quantify the extent and describe the nature of population fluctuations, and identify stable and fluctuating components of the avifauna. In doing so, we seek to answer the following questions: a. to what extent and how can the avifaunal assemblage, and components of it, be characterised as stable or fluctuating? b. how are fluctuations related to antecedent rainfall? and c. what species exhibit relatively stable populations?

2. Materials and methods

2.1. Study area

Newhaven Wildlife Sanctuary (22°42′S, 131°09′E) is a 261,000-ha property 350 km west-north-west of Alice Springs within the Great Sandy Desert bioregion in central Australia. The Sanctuary is owned by Australian Wildlife Conservancy (AWC), who manage the property for conservation, with active fire management, feral animal and weed control programs. Stock from a previous holding as pastoral lease were removed from Newhaven by 2003. The property consists predominantly of semi-desert sandplains, dunefields, quartzite ranges and outcrops dominated by hummock grass of the genus *Triodia* (Latz et al., 2003). Smaller areas of non-spinifex vegetation communities are present including open salt-bush flats, tussock grasslands over calcrete and gypsum, and mulga (*Acacia aneura*) woodlands. There are also numerous ephemeral saline and freshwater lakes.

Mean and median annual rainfall at the Sanctuary homestead (53 years of data) is 342 and 328 mm respectively, with 76% of rain falling in the six hotter months of October to March ("summer") inclusive. Rainfall is highly variable between months and years, recorded monthly totals having varied from 0 to 400 mm, 3-month totals from 0 to 667 mm, and annual totals from 66 to 951 mm. The northern Australian semi-deserts in which Newhaven is situated have among the highest levels inter-annual rainfall variation in the world (van Etten, 2009).

2.2. Study design, bird censuses, and timing relative to rainfall

Sixty-six monitoring sites were selected to provide replicated, widely dispersed and interspersed representation (Quinn and Keough, 2002) of the twelve main vegetation communities (5 or 6 sites per habitat; Table S1) in Newhaven Wildlife Sanctuary. All sites were more than 2.5 km from an artificial water source. For the purpose of bird surveys, each site consisted of a 2-ha plot (the