



Original Research Article

Identifying ecological and life-history drivers of population dynamics of wetland birds in South Africa

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ABSTRACT

Identifying species most vulnerable to environmental change requires reliable estimates of population trends and identification of traits that tend to be associated with these trends. Using state-space models that explicitly describe how the population size changes over time, we estimated population trends of 25 non-migratory African, 13 intra-African migrants, and 16 Palearctic migratory waterbird species during 1995–2009 in South Africa. Using the average of the slope of the last five years (2005–2009), we used phylogenetic generalized least squares analyses to identify relationships with life-history (parental care, extent of polygamy, chick development, body size, average brood size) and ecological traits (migratory status, breeding latitude, foraging guild, wintering habitat type). The significant predictors of population trend were migratory status, average brood size, type of chick development (altricial, semiprecocial, precocial), and extent of male polygamy (0%, = <20%, >20%). Long-distance Palearctic migrants and African non-migratory species on average suffered the greatest magnitude of decline, intra-African migrants showed population increase. There was a negative relationship between population trend and average brood size with an increase in brood size resulting in negative trends. Altricial species and species with some extent of polygamy (= <20%) had the greatest population increase. Our results provide evidence that these recent population trends were non-random with respect to life-history traits.

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1. Introduction

Identifying the species most vulnerable to human and climate-induced changes requires two approaches: first, a reliable estimate of the population size and trend and, second, the identification of possible ecological pressures and life-history characteristics that account for observed trends (Okes et al., 2008). How do we estimate population size and approximate population change as accurately as possible, given that raw counts are typically subject to considerable observation error? State-space models (Buckland et al., 2004; Durbin and Koopman, 2001) are increasingly being used in the modelling of wildlife

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population dynamics (Newman et al., 2014). The underlying basis of this framework is that a true but unknown population size can be modelled with the state process linked to the observed counts by an observation process (see methods for details).

After estimating population size and trends, identifying relationships between these trends and ecological and life-history traits can give us important information on potential causes for decline. Numerous studies have demonstrated the relationship between life history and environmental traits and population dynamics of avian species. Some morphological and ecological traits significantly affect spatial and temporal functional diversity of waterbirds (Mendez et al., 2012). Large-bodied species are physiologically buffered against environmental fluctuations compared to smaller bodied species (Gaston and Blackburn, 1995; Ricklefs et al., 1996), monogamous species have a higher extinction risk than polygamous species (Saether et al., 2004), smaller clutch size results in increased offspring fitness and survival (Jacobsen et al., 1995; Safriel, 1975), although the reversed was found in precocial species (Lepage et al., 1998). Environmental factors such as dependence on a specific habitat type (Martínez-Abraín et al., 2016), dependence on one or more interspecific interactions likely to be impacted by climate change (Julliard et al., 2004; Kausrud et al., 2008), and hunting pressure (Pöysä et al., 2013) contribute to population decline in some species.

Several projects monitor the status of Palaearctic migrants on both the breeding and non-breeding areas (Sanderson et al., 2006; Wetlands International, 2012). Consequently, population sizes and trends of these species are well known (Wetlands International, 2012). For instance, Wetland International monitors 337 populations of 154 species of European breeding waterbirds and 362 populations of 185 species of African waterbirds. Of the 362 African waterbirds populations, 99 (27%) have unknown trends in contrast, of the 337 populations of European breeding waterbirds 42 (12%) have unknown trends.

Unfortunately, quality census data for waterbirds in Africa are generally very rare, the population status and trends of many species are unknown or, at best, are tentative with a high degree of uncertainty (Okes et al., 2008; Wetlands International, 2012). In response to its obligation to meet monitoring requirements under Wetland International's African Waterfowl Census (now African Waterbird Census) programme, South Africa, through the Animal Demography Unit at the University of Cape Town, launched the Coordinated Waterbird Counts (CWAC) programme in 1991. The project monitors a total of 705 wetlands in South Africa (<http://cwac.adu.org.za/sites.php>) and is the largest wetland monitoring project on the continent.

Because waterbirds depend heavily on wetlands, the global loss and degradation of wetland due to urban development and for recreational purposes (Hughes and Hughes, 1992; Junk, 2002) will impact many species negatively. Within Africa, the situation might be worsened due to the predicted decline in rainfall by up to 15% per decade (DEA, 2013). This threatens the survival of resident species, especially those dependent on inland wetlands, as well as migratory species during the non-breeding part of their annual cycle in Africa. Coastal species are also threatened by 'coastal squeeze' (Doody, 2004), the loss of coastal habitats due to accelerated sea level rise coupled with anthropogenic development and building of storm defences around coastlines (Torio and Chmura, 2013).

Our aim in this study is to provide information on the population trends of resident African species as well as migratory species that winter in Africa. Using the mean slope of the last five years, we determined if population change among different species was related to life-history traits and ecological characteristics.

The following are our working predictions:

1. Long-distance Palaearctic migrants will have the greatest magnitude of decline because their population trend is affected by conditions on the breeding, stop-over, and wintering areas (Newton, 2007; Kirby et al., 2008) whereas intra-African migrants will have the least population change because their nomadic nature allows them to move away from unfavourable conditions to favourable habitats giving them a competitive edge (Dean 2004).
2. Smaller species will experience greater decline because their high metabolic rate and reduced ability to sustain substantial energy reserves compared with larger species makes them less likely to survive unfavourable conditions (Nagy, 2005).
3. Habitat specific species (e.g., strictly coastal or inland species) will experience greater decline than habitat generalists (Thuiller 2003).
4. Population change of species breeding in the taiga (50–60°N) will be different from that of species breeding in the Arctic tundra (60–75°N) because climate change is expected to be fastest in the taiga compared to the Arctic tundra region (Hegerl and Scott, 2014)
5. Monogamous species will have a greater magnitude of decline compared with polygamous species because monogamous species are predicted to have a higher extinction risk than polygamous species (Saether et al., 2004)
6. Altricial species will experience a greater magnitude of decline compared with precocial species

2. Methods

2.1. Census data

We used waterbird counts from 16 wetlands in the Western Cape Province, South Africa for this study (Supplemental material Table S1). The wetlands surveyed include marshes, lakes, rivers, estuaries and lagoons, stretches of coastline, salt-pans, and reservoirs. With the term waterbird, we refer to all non-passerines normally associated with wetland habitats. Waterbirds were counted every six months in January/February (austral summer) and June/July (austral winter). The method

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