



## 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

of counting for a particular site is standardized, i.e., the area covered and the counting protocol was constant within sites and from count to count. Standardization between sites was not possible because of the variation in the size of the sites, and logistics; observers on foot counted some sites while boats or vehicles were used at other sites.

Larger wetlands are divided into sections and a team of two counted the wetland birds in each section. As much as possible, the counts of all section start and end at approximately the same time. Teams in adjacent sections will walk in the same direction; e.g., teams will start at the north end of their section and move south. To avoid double counting, when a flock of birds fly into any section from behind the counters, it is not recorded. Full details of the count protocol and wetlands covered under this project are available at the CWAC website (<http://cwac.adu.org.za/>).

The availability of time-series data differed between sites, some wetlands having counts dating back to the 1980s while some sites have only been counted regularly from the 1990s. We restricted our analysis to the period 1995 to 2009 when there were no missing counts and when data were available for all 16 sites. The counts at all 16 sites were usually carried out within the same period; there is usually a maximum difference of five weeks between the earliest and the latest counted site each year. We assume that the total population across these sites equals the sum of the populations at the individual sites.

## 2.2. Population trend analysis

We constructed a state-space model to estimate population size and trends (Harvey, 1989). By using state-space models we separate observation error from the long-term changes in the underlying population size (process error), thereby obtaining better uncertainty estimates for population size and population trends (Durbin and Koopman, 2001).

There are several advantages to using state-space models over traditional linear and non-linear methods. One is that process noise can be separated from observation error and the models provide smoothed estimates of the population size over time, thereby improving our ability to describe trends (Humbert et al., 2009; Valpine and Hastings, 2002). This is particularly important if there is large observation error, as is to be expected in wildlife count data. Another feature is that we can explicitly model how the population size and slope change over time (Simmons et al., 2015). Finally, state-space models allow for fitting multivariate time series (Simmons et al., 2015) and this is important when analysing multiple related time series especially when the parameter estimates of one of the series depend on another. This feature is pertinent to our study because our data consist of two counts per year, one in summer and one in winter.

A state-space model is defined by two parts: one for the population dynamics (state) and one for the observations. The species in our sample differ in their summer-winter movement ecologies, therefore, we used two models to capture the different mechanisms that lead to seasonal fluctuations. We fitted all models to log-transformed counts. We estimated the mean population size and trend of 38 resident and 16 migratory species (Supplemental material Table S2). These were the species with 10 or more individuals per count; this criterion was applied to keep the assumption of log-normality realistic.

## 2.3. Model 1: sedentary residents with limited or no seasonal movement between sites

For these species we fitted a univariate model with summer/winter as a covariate (Fig. 1a).

**Observation (count) process** at time  $t$  is defined by the equation:

$$\ln(y_t) = \mu_t + \gamma_t + \alpha_t, \quad \alpha_t \sim N(0, \sigma_\alpha^2)$$

where  $\ln(y_t)$  is the logarithm of the count,  $\mu_t$  is the logarithm of the unobserved (relative) population size,  $\gamma_t$  is the seasonal effect, and  $\alpha_t$  is the observation error.

For the state process we assumed a local linear trend model:

$$\ln(\text{relative population size at time } t) : \mu_t = \mu_{t-1} + \beta_{t-1} + \omega_t, \quad \omega_t \sim N(0, \sigma_\omega^2)$$

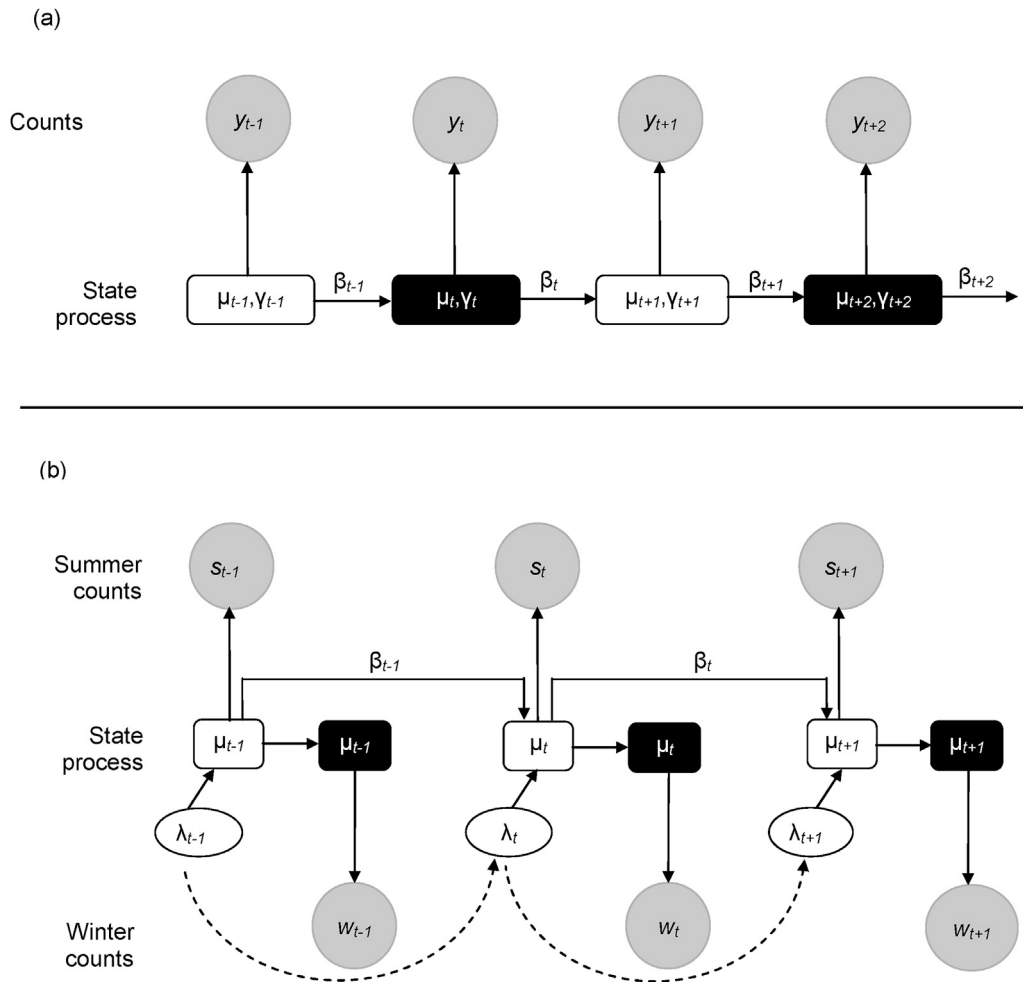
The change in the population size is determined by time-varying slope term  $\beta_t$ . The slope and seasonal effects are modelled as:

$$\ln(\text{population change}) : \beta_t = \beta_{t-1} + \varepsilon_t, \quad \varepsilon_t \sim N(0, \sigma_\varepsilon^2)$$

$$\ln(\text{seasonal effect}) : \gamma_t = -\gamma_{t-1} + \zeta_t, \quad \zeta_t \sim N(0, \sigma_\zeta^2)$$

All error terms  $\alpha_t$ ,  $\omega_t$ ,  $\varepsilon_t$ , and  $\zeta_t$  are normally distributed, serially independent and independent of each other.

An example of a species for which this model was used is Kittlitz's Plover *Charadrius pecuarius* (Fig. 2). This species can move relatively short distances between networks of wetlands but essentially remains close to a specific wetland for most of the year (Lipshutz et al., 2011).

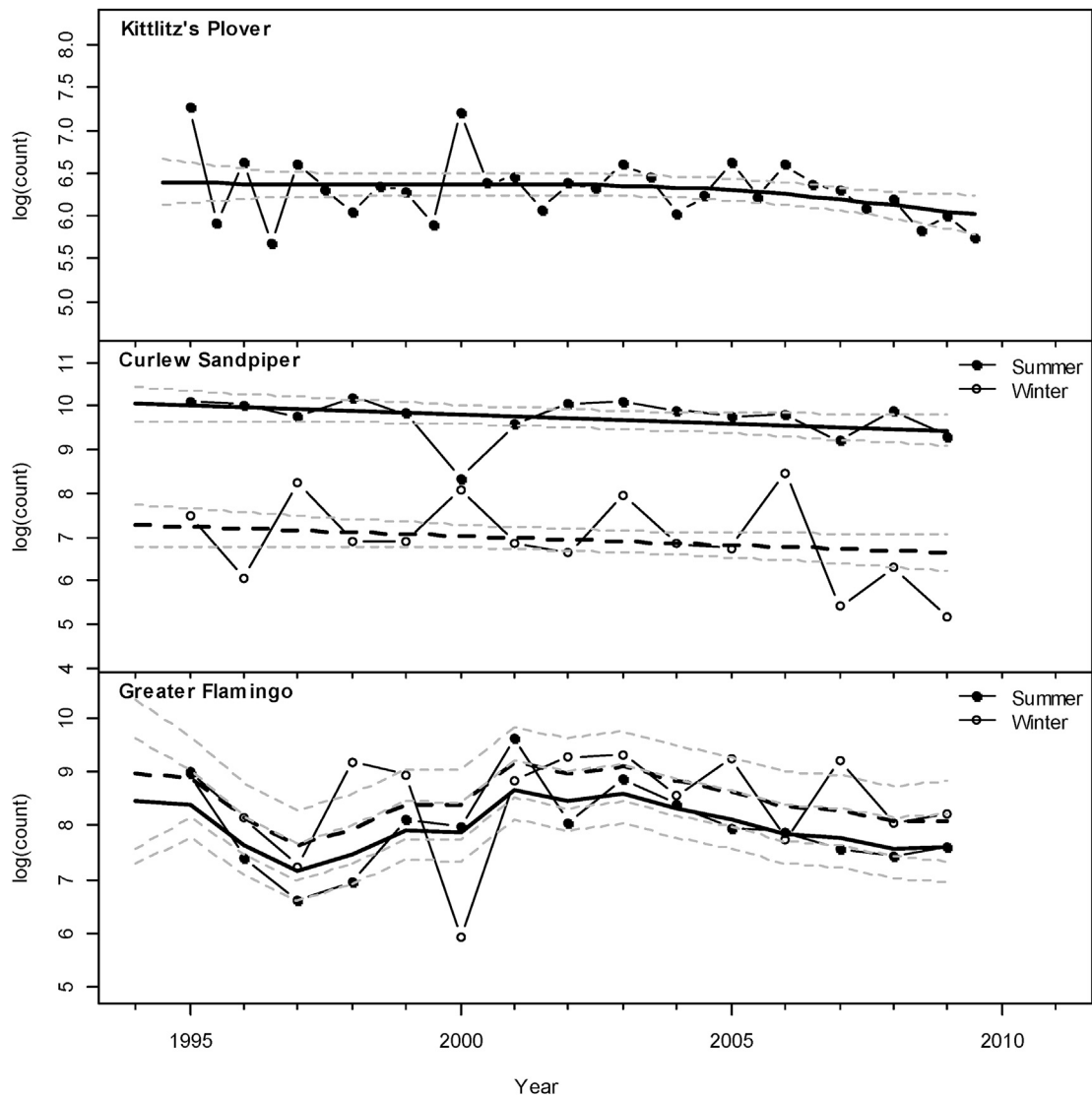


**Fig. 1.** Representation of the univariate (a) and bivariate (b) state-space models used to estimate population size and trends of waterbirds in South Africa. Solid white square boxes represent summer population size, solid black square boxes represent winter population size, grey circles and arrows represent observations (counts). Key to symbols:

- $y_t$  = observation representing both summer and winter counts for the univariate model
- $s_t$  = summer count
- $w_t$  = winter count
- $\gamma_t$  = seasonal effect
- $\mu_t$  = population level
- $\beta_t$  = slope
- $\lambda_t$  = winter ratio (ratio of winter in relation to summer population size –or vice versa–on log-scale)

#### 2.4. Model 2: palaeartic migrants and intra-African migrants

In many Palaearctic migrants, e.g. Curlew Sandpiper (*Calidris ferruginea*), which breed in the northern hemisphere and migrate south for the southern summer, some, mostly young birds, remain at the non-breeding sites during the subsequent southern winter. For these species, we modelled southern summer and winter counts as a bivariate time series in which the summer population size at time  $t$  is the state variable of main interest, and the winter to summer population size ratio (a difference on the log scale) was modelled to introduce dependence between the winter and summer time series (Fig. 1b; Fig. 2). Our state-space model is then:



**Fig. 2.** Population trends of Kittlitz's Plover, Curlew Sandpiper, and Greater Flamingo in South Africa (1995–2009) estimated using univariate (model 1 in text) and bivariate (model 2 in text) structural time series models. Black lines shows the smoothed population estimates, the dashed grey lines indicate the upper and lower limits of the 95% confidence interval.

#### Observation process model

$$\ln(\text{summer count}) : s_t = \mu_t + \alpha_t, \quad \alpha_t \sim N(0, \sigma_\alpha^2)$$

$$\ln(\text{winter count}) : w_t = \mu_t + \lambda_t + e_t, \quad e_t \sim N(0, \sigma_e^2)$$

where  $\lambda_t$  is the log of the winter to summer population size ratio.

#### State process model

$$\ln(\text{summer population change}) : \mu_t = \mu_{t-1} + \beta_{t-1} + \omega_t, \quad \omega_t \sim N(0, \sigma_\omega^2)$$

$$\ln(\text{population change}) : \beta_t = \beta_{t-1} + \zeta_t, \quad \zeta_t \sim N(0, \sigma_\zeta^2)$$

$$\ln(\text{winter to summer ratio}) : \lambda_t = \lambda_{t-1} + \varepsilon_t, \quad \varepsilon_t \sim N(0, \sigma_\varepsilon^2)$$

where  $\alpha_t$ ,  $e_t$ ,  $\omega_t$ ,  $\zeta_t$ , and  $\varepsilon_t$  are error terms serially independent, and independent of each other. This is the model used by Simmons et al. (2015).

Some partial African migrants also show seasonal patterns of movement with high numbers recorded within the Western Cape of South Africa during the summer months and lower numbers during the winter (e.g., Pied Avocet *Recurvirostra avosetta*). In other cases, some species such as Greater Flamingo *Phoenicopterus roseus* show the reversed pattern with high numbers in winter and low numbers in summer (Hockey et al., 2005). To these we also fitted model 2 (Fig. 2).

We fitted the above models to the counts of each species combined from all 16 sites. The goal was to get regional trends rather than site-specific trends. The state-space models were fitted with package dlm v1.1-4 (Petris, 2009; Petris et al., 2013) for the R software v3.0.1 (R Core Team, 2013) using Kalman filtering (Petris et al., 2013). The state-space models give us year-specific estimates of population size for each species, and yearly estimates of population changes.

## 2.5. Factors affecting population change

From the estimated population trends, we used the five-year averages of the slope for the period 2005–2009 as an indicator of recent population change. For migratory species, we used the five year average of the slope of either summer or winter depending on which one represents the main population level. Because slope ( $\beta$ ) estimates were on a log scale, the arithmetic mean of  $\beta$  was exponentiated to obtain the (geometric) mean population rate of change. The magnitude of the population change is significant if the confidence intervals do not overlap with zero.

For each species, we compiled information on average body size (cm), average brood size, parental care, chick development, extent of male polygamy, extent of female polygamy, functional groups, breeding latitude (of migratory species), and habitat with which each species is associated (detailed description of traits in Table 1). The choice of life-history and ecological traits used was, unfortunately, limited by availability of information for most species. To determine the factors related to population trend, we used a phylogenetic generalized least square (PGLS) implemented in the phytools package (Revell, 2015) in R. PGLS uses an estimate of phylogenetic correlation (Pagel's lambda) and controls for this non-independence due to phylogeny in a generalized least squares framework. The phylogeny was taken from birdtree.org (<http://birdtree.org/>) and follows the Birdlife V7 world list (June 2014). We used non-African congeners as surrogates for two species: Purple Swamphen *Porphyrio madagascariensis* (congener: *Porphyrio porphyrio*) and Little Grebe *Tachybaptus ruficollis capensis* (congener: *T. r. ruficollis*).

We built two models: one related to environmental traits and the second related to the intrinsic life-history traits of the species. In the first model, we examined relationships between population trends and migratory status, foraging guild, habitat type used most by each species (coastal, inland, mixed), and breeding latitude (for migratory birds). In the second model, we examined relationships between the population trends and body size, brood size, type of chick development, extent of male and female parental care, and extent of male and female polygamy.

**Table 1**  
Ecological and life-history traits used for the phylogenetic analysis.

Trait	Description
Migratory status (factor)	African non-migratory residents, intra-African migrants, and Palaearctic migrants
Breeding latitude (Factor)	The breeding latitude of Palaearctic migratory species (taiga or Arctic tundra). The reason the breeding latitude for African species was not used was because all the resident species in the Western Cape breed at the same latitude (−33.91) while the breeding latitude of most intra-African migrants was unknown
Parental care (factor)	Species are classed as either having a single- or bi-parental care system
Extent of polygamy (Ordinal)	Male polygamy (MP); Female polygamy (FP). 0 = no polygamy; 1 = polygamy in <20% of breeding population; 2 = 20% or more polygamy of breeding population.
Chick development (Ordinal)	0 = altricial (chicks unable to walk, depend on parents for feeding); 1 = semiprecocial (chicks able to walk within hours of hatching, but still rely on parents for feeding); 2 = precocial (chicks leave the nest and can forage within a few hours of hatching).
Body size (Scale)	Measure of average body size (head to tail in centimetres) for that species.
Average brood size (Scale)	The average number of eggs nurtured by the species. In cases where two eggs are laid but only one typically makes it to maturity, the average brood size was one.
Foraging guilds (factor)	Based on their use of foraging habitat within a wetland, classed as: a = short vegetation or mud including grass, b = shallow water, and c = in or over deep water (modified from Cumming et al., 2012)
Habitat type with which species are typically associated	coastal, inland freshwater, or mixed (generalists found at both coastal and inland wetlands)

### 3. Results

In total, we produced population trends from 1995 to 2009 of 54 species (Supplemental material Figures S1-3). The population sizes and trends of 25 resident species were estimated using model 1 (Supplemental material Table S2 and Figure S1). The mean geometric mean of the slope in 2005–2009 of thirteen species showed declining population trends but only the decline of the Maccua Duck (*Oxyura maccoa*) was statistically significant 0.85 (0.36; 0.91), 12 had stable or increasing trends but only the increase of the Black-headed Heron (*Ardea melanocephala*) was statistically significant 1.13 (1.05; 1.54).

The population trends of 16 Palaearctic migrants and 13 intra-African migrants were estimated with model 2 (Supplemental material Figure S2 and S3). The mean geometric mean of the slope in 2005–2009 of eleven of the Palaearctic migrants showed declining trends, six were statistically significant. The species with statistically significant trends were the Eurasian Curlew *Numenius arquata* (18%), Marsh Sandpiper *Tringa stagnatilis* (17%), Red Knot *Calidris canutus* (12%), Ruddy Turnstone *Arenaria interpres* (6%), Terek Sandpiper *Xenus cinereus* (17%), and Wood Sandpiper *Tringa glareola* (15%). Five of the Palaearctic migrants had statistically non-significant population increases (Supplemental material Table S2, Figure S2). Among intra-African migrants, the South African Shelduck (*Tadorna cana*) and Southern Pochard (*Netta erythrophthalma*) had population declines (not statistically significant). All other species had increasing trends, although only for the Greater Flamingo (*P. roseus*), Lesser Flamingo (*Phoeniconaias minor*) and Spur-winged Goose (*Plectropterus gambensis*) were these statistically significant (Supplemental material Table S2, Figure S3).

Combined, the 16 wetlands surveyed in this study hold greater than 1% of the global or sub-Saharan populations of African Black Oystercatcher, Black-necked Grebe, Black-winged Stilt, Cape Shoveler, Chestnut-banded Plover, Curlew Sandpiper, Greater Flamingo, Grey Plover, Lesser Flamingo, Pied Avocet, Ruddy Turnstone, Sanderling, and White-fronted Plover (Supporting Table S3).

#### 3.1. Population changes related to ecological and life-history traits

Geometric mean of the annual population change in 2005–2009 differed significantly between the three migratory groups (Table 2). Pairwise comparisons showed that the average population change of intra-African migrants differed significantly from that of Palaearctic migrants and non-migratory residents but the difference in population change of Palaearctic migrants and non-migratory resident species was not significant (Fig. 3). Foraging guild and habitat each species typically used on the non-breeding areas and breeding latitude of migratory species were not significant predictors of population trends (Table 2).

After controlling for migratory status, the average brood size, extent of chick development and male polygamy were significant predictors of population change (Table 3). The relationship between population trend and brood size was a negative one, species having a larger brood size had declining population trends compared with species with smaller broods (Fig. 4). The extent of chick development also significantly predicted population change. Species with altricial chicks showed the greatest population increases compared with species with precocial and semiprecocial chicks (Table 3).

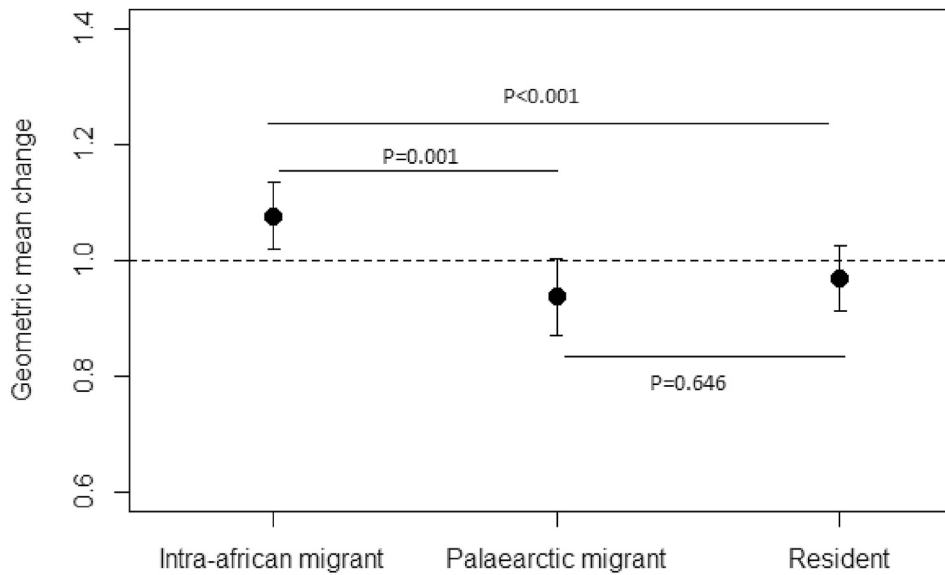
### 4. Discussion

The dynamics of waterbirds in Africa has often been perceived as a “black box”; not much information is available on the population dynamics of Palaearctic migrants in the African wintering quarters and even less information is available for the population dynamics of resident African species. Our study provides previously unknown population trends of 11 species: the African Spoonbill, Black-winged Stilt, Common Moorhen, Great Crested Grebe, Little Grebe, Great White Pelican, Kittlitz's

**Table 2**

Results of the phylogenetic regression of population changes on ecological traits in African non-migratory, intra-African migrant, and Palaearctic migrant waterbirds in South Africa.

Parameters	Marginal means (CI)	F	P
Status		10.07	<0.0001
Intra-African migrants	1.07 (1.01; 1.13)		
Palaearctic migrant	0.93 (0.87; 1.00)		
Non-migratory resident	0.96 (0.91; 1.02)		
Foraging guilds		0.92	0.411
a	1.02 (0.97; 1.06)		
b	1.01 (0.95; 1.06)		
c	0.95 (0.87; 1.03)		
Habitat		1.13	0.330
Coastal	0.96 (0.89; 1.02)		
Inland	1.00 (0.93; 1.08)		
Mixed	1.01 (0.96; 1.05)		
Breeding latitude		0.72	0.361
Arctic tundra	1.01 (1.003; 1.02)		
Taiga	0.99 (0.95; 1.03)		



**Fig. 3.** Difference in mean annual population change between resident, intra-African migrants, and Palaeartic migrant waterbirds in South Africa.

**Table 3**

Results of the phylogenetic regression of population changes on life history in African non-migratory, intra-African migrant, and Palaeartic migrant waterbirds in South Africa.

Parameters	Marginal mean (CI)	F	P	$\beta^a$ (SE)
Migratory status		190.2	<0.0001	
Parental care		2	0.1843	
Both	1.06 (1.004; 1.13)			
Single	0.99 (0.87; 1.11)			
Chick development		131	<0.0001	
Altricial	1.07 (1.008; 1.13)			
Semiprecocial	1.001 (0.93; 1.06)			
Precocial	1.02 (0.96; 1.08)			
Male polygamy		6	0.0072	
0	0.94 (0.82; 1.07)			
1	1.13 (1.05; 1.22)			
2	1.009 (0.89; 1.11)			
Female polygamy		2	0.2045	
0	1.07 (1.02; 1.12)			
1	1.06 (0.97; 1.14)			
2	0.96 (0.8; 1.11)			
Average brood size		9	0.004	-0.014 (0.004)
Body size (cm)		0.0001	0.830	-0.00006 (0.0002)

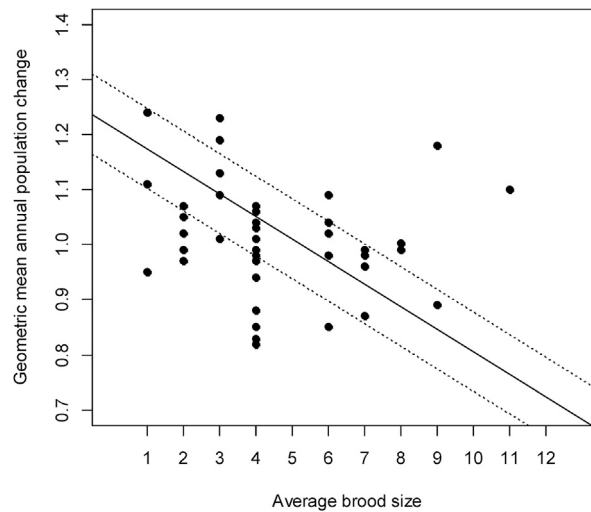
<sup>a</sup>  $\beta$  refers to the slope estimate of continuous variables.

Plover, Three-banded Plover, Water Thick-knee, White-fronted Plover, and Yellow-billed Duck. Our results show that the Palaeartic migrants showed the largest population declines agreeing with results observed at breeding or stop-over sites (Busche, 2011; Sanderson et al., 2006). That the non-migratory resident species showed similar average population decline as the Palaeartic migrants suggested that deteriorating conditions at the austral end might be contribute to declines even though we did not find a statistically significant relationship between the magnitude of population change and ecological variables considered in this study. Intra-African migrants on the other hand did not show declines over the same period indicating that their ability to move with changing conditions gave them a competitive advantage over long-distance migrants and non-migratory residents. This mirrors the finding of Sanderson et al. (2006) who found that in European breeding birds, Afro-Palaeartic migrants showed steeper declines compared to short distance migrants. In total, four resident African species and five Palaeartic migrants showed evidence for statistically significant changes in population size.

#### 4.1. Notes on some species

In the African species with statistically significant population changes, the population of the Greater Flamingo, Maccoa Duck, and the Black-headed Heron show an increasing trend, reflecting the population trends reported for the continent or sub region. The increased populations of the Lesser Flamingo was the reverse of the trends reported for the southern Africa





**Fig. 4.** Relationship between average brood size and mean population change (solid black line) of resident waterbirds in South Africa; dashed lines are 95% confidence intervals.

region. Our results indicate a five year (2005–2009) average summer population increase of 24% in the Western Cape. The IUCN (2014) classifies Lesser Flamingo population as ‘vulnerable’ owing to the steady long-term population declines reported across its range in eastern and southern Africa and Simmons (1996) reported a 50% decline across the entire southern region. Between 2001 and 2012, however, the population has remained stable at 55,000–65,000 breeding pairs (Wetlands International, 2012). This increase in Lesser Flamingo population might be due to the concerted efforts to protect and increase the breeding sites of the species at Kamfers Dam in South Africa resulting in an annual breeding output of >20,000 chicks annually since 2012 (Anderson, 2008). The 13% population increase in the Black-headed Heron, and the 18% increase in the Spur-winged Goose agree with the trends reported across the species’ range (BirdLife International, 2013). Reasons for population increases have been attributed to increase in new suitable wetland habitats (Scholte, 2006) and an expansion of range owing to man-made pastures, dams, and reservoirs (Turner, 2011).

We recorded an (five-year) average annual decline of 15% for the Maccoa Duck. The IUCN classifies this species as ‘near threatened’. The southern population of the Maccoa Duck, the largest for the continent, was originally considered to be stable and even increasing (Berruti et al., 2005) but after a review of its population size, it was later determined that the species may have been undergoing a steady decline (Abebe et al., 2006). The main causes of decline are pollution, habitat loss, and changes in water levels which disrupt breeding activities (Berruti et al., 2005). Although not statistically significant, it is also worth noting that the Southern Pochard and South African Shelduck show a 13% and 11% population decline respectively in the Western Cape. While these are common and wide-spread species with previously reported increasing or stable populations (Wetlands International, 2012) this declining trend in the 2005–2009 period could be an early warning of the species’ population trend in the region.

For Palearctic migrants, our results confirm earlier studies which reported major declines in the populations of Red Knot and Ruddy Turnstone in South Africa (Harebottle et al., 2006) and Namibia (Simmons et al., 2015). We also recorded significant declines in populations of Eurasian Curlew, Marsh Sandpiper, Terek Sandpiper, and Wood Sandpiper. Because South Africa is the southernmost limit of the wintering range of these species on the Palearctic–Afrotropical flyway, population declines would be first detected in this region; these trends might be an indication of the trend for the rest of the flyway. In meadow breeding birds like the Eurasian Curlew and Marsh Sandpiper, agricultural intensification on the breeding areas has resulted in low breeding productivity of these species (Donald et al., 2006). Loss or reduction in quality of habitats on both the breeding and wintering areas (Byrkjedal et al., 2012; Donald et al., 2006), hunting and increased predation (Ims et al., 2011; Kausrud et al., 2008), and possibly increased competition (Brommer et al., 2012; Virkkala et al., 2008) have also contributed to population declines of the migrants.

The population of the Terek Sandpiper which was previously reported as stable for the Palearctic–Afrotropical flyway (Wetlands International, 2012) show a 17%. The decline of the Terek Sandpiper in the Western Cape could be attributed to decline in quality and extent of the seagrass (*Zostera capensis*) beds, the species’ preferred feeding habitat. Aerial photographs indicate a 38% decline in seagrass beds at Langebaan Lagoon between 1960 and 2007 (Pillay et al., 2010) with a corresponding decline in the microinvertebrate communities associated with seagrass.

#### 4.2. Predictors of population change

Our results showed that average brood size, extent of male polygamy, and the extent of chick development influenced population change. In many bird species, clutch size affects an individual’s capacity to raise offspring although the cost is

higher in altricial species. In waterbirds this is especially important because extra energy needed for the production of an egg in is about 200% their basal metabolic rate (Carey, 1996). A bulk of the diet of waterbirds is composed of invertebrates, amphibians, and molluscs (Hockey et al., 2005); these prey items are particularly susceptible to extreme weather conditions such as flooding, heatwave, or extreme drop in temperature. There is evidence that inter-annual variability in rainfall pattern in South Africa has increased since the late 1960s (Fauchereau et al., 2003); in particular, droughts and flooding events have become more intense and the switch between the two extremes have become widespread (Mason et al., 1999). In the Arctic and sub-Arctic regions, the peak period of arthropod abundance has advanced in the last three decades due to climate change (McKinnon et al., 2012; Tulp and Schekkerman, 2008). The changes in freeze–thaw cycle has also reduced survival of insects (Sinclair et al., 2003; Turnock and Fields, 2005). All these factors reduce the predictability of food during the breeding seasons affecting these species' ability to successfully raise their young. A large clutch size, which in the evolutionary past may have conferred an advantage to certain species (Both et al., 1998; Lack, 1946), may now be a handicap.

Altricial, semiprecocial, and precocial species all showed a population increase (7%, 1%, and 2%, respectively) although only altricial species had statistically significant increase (Table 3). Although altricial species require intensive parental care, chick growth and fledging is fast (Starck and Ricklefs, 1998) allowing the parents to potentially raise more than one brood within a season. In many precocial species, while parental investment is minimal, the period of chick growth is usually long with lengthy parental investment in the form of brooding and defence against predators (Naef-Daenzer and Gruebler, 2016).

Although we found a relationship between population change and an intermediate level of polygamy in males (Table 3), we suspect that this result might be spurious due to uneven sample size for the three levels of polygamy. Our sample had 45 monogamous species, six species with polygamy level  $\leq 20\%$ , and three have polygamy level  $>20\%$ . Never-the-less, in some species of birds, polygamy increases fertilization success and may buffer against extinction risk (Rossmanith et al., 2006; Saether et al., 2004; Zeh and Zeh, 2001).

## 5. Conclusion

In conclusion, our study confirmed trends of some species reported on either the breeding or wintering areas, provided updated trends of some species, and new information on the trends of some African species. Our results emphasizes the importance of monitoring the populations of Palaearctic and intra-African migrants at the end of their migration corridor because this could serve as an early warning system for population trends of these species on their flyway. Our results emphasise the importance of the Western Cape wetlands in supporting and probably maintaining significant numbers of some of the species considered in this study. Yet, of the 16 wetlands, only three have full protection status, four partial protection, and nine are unprotected. Many of these sites are threatened by pollution from residential and industrial development, eutrophication, alien vegetation encroachment, and siltation which could severely threaten the populations of the waterbird species that utilize these wetlands. Management of man-made wetlands, such as controlling water level to provide optimum feeding and breeding conditions, especially for the species at risk should be part of management plan. There is also a need for cross-continent collaborations to monitor the populations of intra-African migrants. An example is the Maccoa Duck technical working group, a collaboration between scientists in southern and eastern Africa, which has improved the knowledge of the status of the species in Africa (Berruti et al., 2005).

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.gecco.2017.09.001>.

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