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Original Research

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Waterbird community changes in the Wilderness Lakes, South Africa (Part 2 of 3): Shorebirds

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Scan this QR code with your smart phone or mobile device to read online. Globally, many shorebirds, particularly the smaller migratory waders are declining, which can be attributed to multiple factors throughout their ranges. The Wilderness Lakes Complex in South Africa comprises two estuarine systems, that support diverse waterbird communities, including 17 abundant shorebirds. The study aimed to document long-term spatial and temporal patterns of abundance of shorebirds in the Wilderness Lakes Complex, and where possible identify potential causes for observed trends. The abundance of waterbirds on these wetlands was determined biannually from 1992 to 2019, with counts conducted from a boat following a standardised route. Historical abundance data from the 1980s were also used to describe long-term abundance changes. Ten shorebirds showed seasonal differences in abundances. Significant long-term decreases in abundance have occurred in seven shorebirds (Wood Sandpiper Tringa glareola, Marsh Sandpiper Tringa stagnatilis, Curlew Sandpiper Calidris ferruginea, Ruff Philomachus pugnax, Grey Heron Ardea cinerea, Greater Flamingo Phoenicopterus ruber, Black-winged Stilt Himantopus himantopus) and increases in three species (African Spoonbill Platalea alba, Little Egret Egretta garzetta, Glossy Ibis *Plegadis falcinellus*). Similar types of population changes occurred across multiple waterbodies and in different seasons. The similarity of shorebird abundance trends in spatially separated wetlands suggests either high interconnectivity of populations between wetlands systems and/or prominent drivers of change being broad scaled rather than system specific. Local reasons for changes potentially include the increasing spread of emergent macrophytes and resultant loss of open sandbanks, changing hydrodynamics, and alien fish proliferation, all likely changing food accessibility, as well as periodic high disturbance by waterbody users.

Conservation implications: Changes in the abundances of several shorebirds, particularly small migratory waders, are substantial, with multiple likely local, regional and international drivers acting accumulatively. Recommended corrective actions include continuing involvement in the development and implementation of policies for waterbird conservation, and local management of emergent macrophytes, disturbance, and water level variability.

Keywords: Touw system; Swartvlei system; waterbird community change; species abundance; causes of change; wetlands; waders.

Introduction

Shorebirds rely on shallow water and the wet littoral edges of wetlands for feeding opportunities. Wetlands, however, are globally among the most utilised, modified and transformed habitats, with natural wetland loss estimated to be as high as 87% (Davidson 2014:940), with most remaining wetlands affected to some extent by human activities. Man-made or artificial wetlands, which have proliferated over the past century, may in some instances provide alternative resources for waterbirds (Froneman et al. 2001:267; Harebottle et al. 2008:161). However, they are unlikely to provide comparable habitats for many species (Ma et al. 2004:340), and particularly those that exclusively utilise coastal and estuarine areas for feeding.

Globally, many shorebirds are declining, particularly many of the smaller, migratory, waders (Simmons et al. 2015:7; Wetlands International 2006; Zöckler, Delany & Hagemeijer 2003), though some resident wader populations appear to be stable or even increasing (Essig 2016).

Assessments undertaken around the turn of the century indicated a decline of approximately 45% (49 of 115) of both African and western Eurasian migratory species (Delany 2003:13; eds. Delany et al. 2009) as well as wader populations on a global scale (Gosbell & Clemens 2006).

More recent assessments have demonstrated that these declines have continued (Wetlands International 2012), though such declines may not always be detectable on a local scale.

Fluctuations in shorebird number and associated population trends can be caused by a variety of factors, effective at scales ranging from global to local. These include climate change, predator-prey cycles, habitat transformation and loss, hunting, fluctuations in wetland attributes, weather conditions, predation, pollution, overharvesting of benthic invertebrates, and disturbance (Burton et al. 2006; eds. Delany et al. 2009; Rakhimberdiev et al. 2011; Sanderson et al. 2006; Stroud et al. 2004; Underhill 1987; Zöckler et al. 2003). Moreover, complex interactions between shorebirds and the availability of their prey can also influence breeding success and mortality rates (Kalejta-Summers, McCarthy & Underhill 2001; Lagos et al. 2008; Rakhimberdiev et al. 2011).

Analyses of population trends for shorebirds require high quality species abundance data, which are not always readily available. Natural fluctuations do occur in wetland habitat conditions. When local wetland conditions are unfavourable for waterbirds, this may prompt local or regional movements to search for suitable habitat (Plissner, Haig & Oring 2000:294). Migrants in particular are vagile, and analyses of waterbird abundances at single sites for short durations will not necessarily track global trends. This poses a challenge in determining the extent or cause of changes in waterbird abundances, and emphasises the value of long-term assessments to distinguish between short-term variability and long-term trends.

The objectives of this study were to: (1) identify long-term trends and seasonal patterns for frequently occurring and abundant shorebirds within the Wilderness Lakes Complex (WLC), (2) where possible, identify potential causes for observed trends and (3) consider the conservation implications of observed spatial and temporal changes. This entailed examining seasonal differences in the abundance of species; assessing changes in the abundance of species between surveys conducted in the periods 1980–1983 (Boshoff, Palmer & Piper 1991) and 1992–2019; and examining the occurrence of trends in species abundances in summer and winter surveys for a 28-year (1992–2019) survey period.

Research methods and design Study site

The WLC is situated along the southern coast of South Africa in the Western Cape province, and comprises two estuarine systems, the Touw and Swartvlei. The Touw system consists of three interconnected estuarine lakes (Rondevlei, Langvlei, Eilandvlei) and the Touw Estuary. The Swartvlei system consists of Swartvlei Lake and Swartvlei Estuary. Both estuaries are naturally temporarily open/closed waterbodies. The Touw Estuary is artificially breached when water levels are between 2.2 m and 2.4 m above mean sea level (amsl), and Swartvlei Estuary when water levels are approximately 2.0 m amsl, which in both instances are substantially below that which would potentially be achieved if breaching were to occur naturally (±3.5 m amsl). Reduced freshwater inputs and artificial breaching have resulted in reductions in the percentage of time both the estuaries are open, with Touw Estuary now (1991-2019) being open 28% of the time, and Swartvlei Estuary being open 55% of the time (South African National Parks [SANParks] unpublished data). Six rivers flow into the lake system (Figure 1). The lower catchments of the larger perennial rivers (Touw, Hoëkraal, Karatara), and majority of the catchments of the smaller intermittently flowing rivers (Duiwe, Langvlei Spruit, Klein Wolwe) are intensively utilised for agriculture, plantations and urban development (Filmalter & O'Keeffe 1997).

Dissolved inorganic nutrients (NOx-N, NH4-N and PO4-P) in the Touw system are variable though typically low, with external catchment fluxes likely not the dominant drivers of long-term nutrient patterns in the lakes (Taljaard, Van Niekerk & Lemley 2018:65).

Submerged macrophytes occur in all waterbodies in the WLC, though are generally confined to waters less than 3.0 m deep (Whitfield 1984). Emergent aquatic plants occur on the margins of the lakes. The fish fauna consists of a combination of estuarine (Russell 1996; Whitfield 1984) and alien freshwater species (Olds et al. 2011). The WLC regularly supports populations of up to 68 waterbird species (Randall, Randall & Kiely 2007).

The WLC forms a component of the Garden Route National Park. The Touw system, excluding Touw Estuary, is a designated Ramsar site (Randall 1990). Recreational fishing and boating are permitted on all estuaries and lakes except Langvlei and Rondevlei. Walking is possible and permitted along portions of the shorelines of Touw and Swartvlei estuaries.

Waterbird counts

Assessments of changes in waterbird abundances were based on waterbird counts undertaken in two separate surveys periods.

Firstly, monthly waterbird counts in all waterbodies in the WLC, with the exception of Touw Estuary, were undertaken for 4 years (January 1980 to December 1983) by staff of the then named Chief Directorate: Nature and Environmental Conservation. These counts were undertaken either by using binoculars from a boat following a fixed route (Swartvlei Lake), using a zoom telescope from fixed shore sites (Eilandvlei, Rondevlei, Swartvlei Estuary) or a combination of these methods (Langvlei) as described in Boshoff et al. (1991). The lead of these surveys, Dr Andre Boshoff, made all of the original waterbird abundance data from these counts

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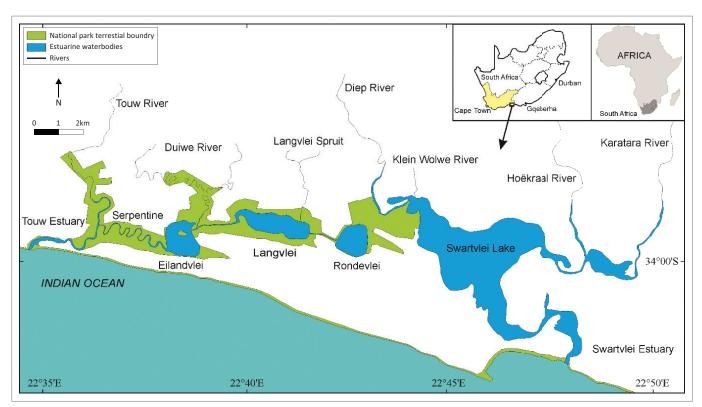


FIGURE 1: Map of study area showing relative position of estuaries and estuarine lakes within the Wilderness Lakes Complex.

available to SANParks in the mid-1990s, for unrestricted use in future assessments of changes in waterbird abundances.

Secondly, waterbird abundances were determined biannually during summer (January-February) and winter (July-August) for 28 years (1992-2019) by the author and coworkers. In the 28-year study period, 56 surveys on each of six waterbodies were undertaken. Counts of all waterbirds were conducted separately on each waterbody by four observers using binoculars, from a boat following a fixed and repeated route parallel to the shoreline of each waterbody. The routes allowed for surveillance of all open water areas on each waterbody, as well as sparsely vegetated and open areas on the waterbody floodplains. Boat speeds were low and stands of dense emergent vegetation supporting high abundances of waterbirds were avoided to minimise disturbance of waterbirds on the water surface. Variability in observer error was minimised by use of the same observers wherever possible throughout the study period, with observers specialising in different taxa. Accurate counts could only be undertaken on days with little or no wind. Online long-term weather forecasts (7 days) were used to select suitable consecutive sample days with little or no wind and low probability of precipitation on four consecutive days within a 3-week window. Counts were undertaken in the morning when wind speeds are typically low, commencing at 08:00, and usually ending at approximately 13:00, with counts undertaken on either one or two waterbodies in a day. In a few instances, when wind speeds unexpectedly increased substantially during surveys, thus reducing the accuracy of counts, the survey was abandoned for the day and restarted

on the next day, or period, with predicted suitable weather. All counts in the entire WLC were conducted over a maximum of four consecutive days in each survey. The scientific and common names of waterbird species are based on those used by Hockey, Dean and Ryan (eds. 2005).

Analysis

The non-parametric Mann–Whitney test was used to assess differences in the abundance of individual bird species in different seasons (summer and winter) using pooled data from all waterbodies collected in the 1992–2019 surveys. The data were tested for normality using the Shapiro-Wilk test.

The mean abundances of waterbirds in four different decades from the years 1980–2019, thus spanning all available waterbird abundance records, were used to assess long-term changes in abundance in the Touw and Swartvlei estuarine systems. Defined decades, and years in which data were collected were the 1980s (data 1980 to 1983), 1990s (data 1990 to 1999), 2000s (data 2000 to 2009) and the 2010s (data 2010 to 2019). To achieve consistency in the calculation of mean abundances across the entire 1980–2019 study period, only data collected in January and July surveys in the 1980s period were used in analyses. Comparisons of species abundances in different decades excluded all data collected on the Touw Estuary as surveys were not undertaken on this waterbody during the 1980s (Boshoff et al. 1991).

The Mann–Kendall trend analysis test was used to determine the significance (p) and direction (increasing or decreasing) of long-term non-seasonal trends in the abundances of waterbirds on both individual waterbodies in the WLC as well as pooled abundance data for the WLC as a whole, with analyses performed separately for summer and winter count data collected in the 1992–2019 surveys.

The selection of reliable estimators of population change is essential in monitoring programmes generating trend data (Ortiz-Velez & Kelley 2023). Zero-inflation resulting from the inclusion of rare species in datasets can bias statistical estimates and trend detection (Cunningham & Lindenmayer 2005), and data screening prior to analysis can typically include exclusion of species with few observations (Thomas & Martin 1996) by setting arbitrary thresholds of percent presence among samples (Ortiz-Velez & Kelley 2023). Count data of only abundant and regularly occurring waterbirds were used in analyses, defined here as those that in the 1992 to 2019 surveys had an average abundance of five or more individuals on at least one waterbody as well as on all waterbodies combined, and were recorded in 50% or more of surveys on at least one waterbody. Trend analyses was not performed on winter abundance data of Palearctic migrants because of their very low abundance or absence in the WLC in winter months. Data were analysed using Systat Version 13 (Systat 2009).

Ethical considerations

This article followed all ethical standards for research without direct contact with human or animal subjects.

Results

Seasonal differences in waterbird abundances

Of the 10 shorebirds that demonstrated seasonal variability in abundance, nine were significantly more abundant during surveys undertaken in summer (Table 1), with only Greater

Flamingo Phoenicopterus ruber being more abundant in winter surveys (U = 214.5; p < 0.002). Ringed Plover Charadrius hiaticula, Wood Sandpiper Tringa glareola, Marsh Sandpiper Tringa stagnatilis, Common Greenshank Tringa nebularia, Curlew Sandpiper Calidris ferruginea, Little Stint Calidris minuta and Ruff Philomachus pugnax are all Palearctic migrants and hence were either absent or occurred in very low numbers during winter. Significantly higher summer abundances occurred for the largely resident Blacksmith Lapwing *Vanellus armatus* (U = 517.0; p < 0.019) and nomadic African Spoonbill Platalea alba (U = 627.0; p < 0.000). The abundance of Grey Heron Ardea cinerea (U = 407.0; p < 0.625), Purple Heron Ardea purpurea (U = 346.0; p < 0.598), Little Egret Egretta garzetta (U = 422.0; p < 0.459), Glossy Ibis Plegadis falcinellus (U = 488.5; p < 0.062), Kittliz's Plover Charadrius pecuarius (U = 365.0; p < 0.825), Pied Avocet Recurvirostra avosetta (U = 422.5; p < 0.408) and Black-winged Stilt *Himantopus himantopus* (U = 367.5; p < 0.860) within the WLC did not differ significantly between summer and winter surveys.

Variation in waterbird abundances between survey periods

Shorebirds could be categorised into one of four groups depending on the pattern of change in abundance across the four decades in the study period. These included: (1) increasing significantly in most or all decades, (2) decreasing significantly over time and particularly with average abundances in the 1980s being higher than in later decades, (3) species with a low-high-low pattern, with significant increases in the decades after 1980s, a high in either the 1990s or 2000s, followed by a decline in the following decade or decades and (4) species with consistently low abundance, and for whom no substantial change in average abundance between decades was apparent.

TABLE 1: Seasonality of shorebirds on waterbodies in the Wilderness Lakes Complex, with species grouped according to season of higher abundance.

Seasonality	Species	Average abundance - Summer								Ave	erage al	oundan	Test statistics for WLC					
		RV	LV	LV EV TE		SL	SL SE		RV	LV	EV	TE	SL	SE	WLC	Mann-Whitney (U)	<i>p</i> <	
Winter	Greater Flamingo	3	0	0	0	0	0	3	11	11	0	0	28	2	53	214.5	0.002	
Summer	African Spoonbill	8	18	0	0	4	2	33	1	3	1	0	3	4	13	627.0	0.000	
	Blacksmith Lapwing	8	11	5	5	6	16	51	4	9	3	3	3	18	40	517.0	0.019	
	Ringed Plover†	1	0	0	0	0	22	24	0	0	0	0	0	0	0	616.0	0.000	
	Wood Sandpiper†	1	3	0	0	0	0	4	0	0	0	0	0	0	0	626.5	0.000	
	Marsh Sandpiper*	3	4	0	0	0	21	29	0	0	0	0	0	1	1	649.0	0.000	
	Common Greenshank†	2	2	0	0	4	39	47	0	0	0	0	0	4	4	695.5	0.000	
	Curlew Sandpiper†	3	5	0	0	1	56	65	0	0	0	0	0	1	1	630.0	0.000	
	Little Stint†	1	6	0	0	0	9	16	0	0	0	0	0	0	0	659.5	0.000	
	Ruff†	24	25	0	0	3	5	57	0	0	0	0	0	0	0	700.5	0.000	
Non-seasonal	Grey Heron	1	3	1	1	3	16	25	2	4	1	2	5	10	23	407.0	0.625	
	Purple Heron	2	3	2	0	2	1	11	2	4	2	1	2	0	12	346.0	0.589	
	Little Egret	8	17	2	1	9	13	50	6	13	3	1	4	23	48	422.0	0.459	
	Glossy Ibis	4	8	0	0	0	0	13	2	3	0	0	0	1	5	488.5	0.062	
	Kittlitz's Plover	4	2	0	0	0	6	12	2	2	0	0	0	8	11	365.0	0.825	
	Pied Avocet	1	3	0	0	1	5	9	1	1	0	0	1	2	5	422.5	0.408	
	Black-winged Stilt	8	25	1	0	6	25	65	6	14	0	0	11	42	73	367.5	0.860	

Note: Average abundances are given of waterbirds on lakes and estuaries in both summer and winter surveys undertaken from 1992 to 2019. Test statistics are given for the seasonal difference in the abundance of waterbirds within the entire Wilderness Lakes Complex for the Mann-Whitney U test where p, probability value.

Palearctic migrants.

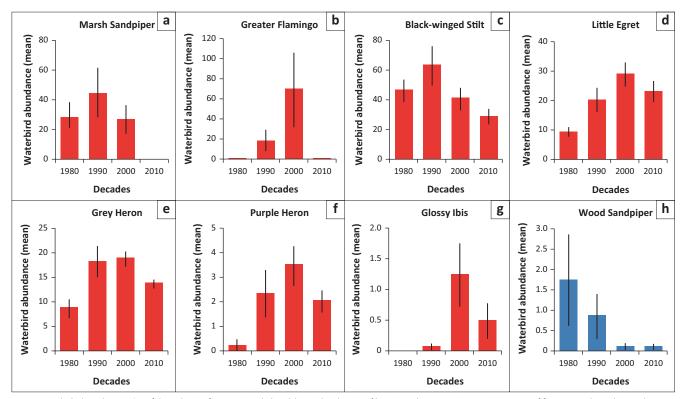
RV, Rondevlei; LV, Langvlei; EV, Eilandvlei; TE, Touw Estuary; SL, Swartvlei Lake; SE, Swartvlei Estuary; and WLC, Wilderness.

Of the 17 shorebirds, seven followed the low-high-low pattern on the Swartvlei system with relatively low abundance in the 1980s, higher abundance in the 1990s (Marsh Sandpiper, Black-winged Stilt) (Figure 2a, Figure 2c) and/or 2000s (Greater Flamingo, Little Egret, Grey Heron, Purple Heron, Glossy Ibis), followed by a decline in the 2010s (Figure 2b, d–g). The decline of Marsh Sandpiper and Greater Flamingo in particular in the 2010s was substantial. Glossy Ibis was not recorded in the WLC prior to the 1990s, and although newly established in the region, has occurred in low abundances on the Swartvlei system (Table 1). The abundance of Blacksmith Lapwing has also undergone a broad low-high-low change in abundance through the decades (Figure 2q) though the overlapping of confidence limits suggests that this trend has not necessarily been significant.

Five of the six shorebirds that migrate annually from Palearctic regions (Wood Sandpiper, Common Greenshank, Little Stint, Curlew Sandpiper, Ruff) have undergone substantial declines in abundance on the Swartvlei system (Figure 2h–l), and particularly Swartvlei Estuary (Table 1). For Wood Sandpiper the overall abundance changes have been relatively small, whereas, for Curlew Sandpiper the changes have been substantial (1980s summer survey average = 657 individuals, declining to four individuals in the 2010s) and in Ruff the decline has been absolute (1980s summer survey average = 19 individuals, declining to zero individuals in the 2010s). The abundance of Pied Avocet in the WLC is highly variable. In some years it is relatively abundant (e.g. 49 individuals recorded in summer 1993), though more typically it occurs in low numbers (<5 individuals) or is absent during waterbird surveys. The resulting high statistical variance from such intermittent occurrence masks what appears to be a decline in overall abundance from the 1980s compared to later decades on the Swartvlei system.

Both Kittlitz's Plover and Ringed Plover have not shown any consistent pattern of abundance on the Swartvlei system, with both undergoing varying and irregular changes in abundances in successive decades. The average abundance of the relatively uncommon African Spoonbill on the Swartvlei system, although exhibiting a slow upwards trend, does not differ significantly between decades (Figure 2p).

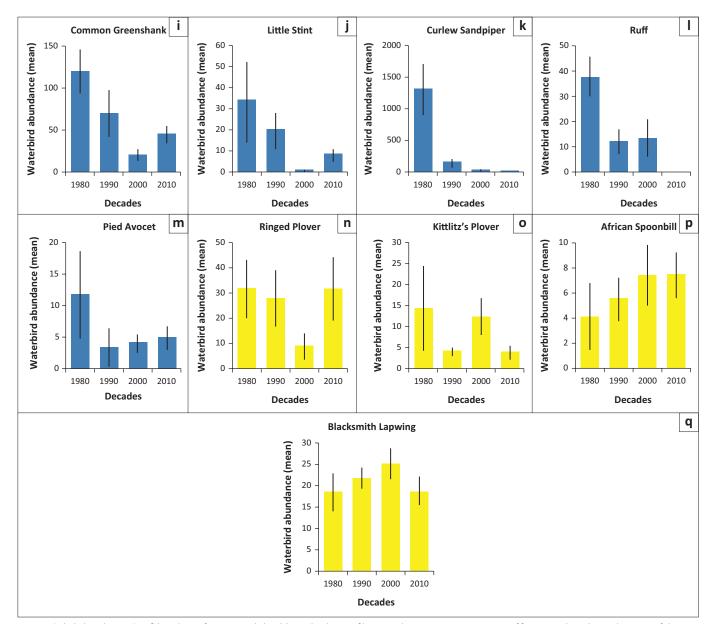
The majority (12) of the considered species, including all Palearctic migrants, have undergone significant declines in abundance on the Touw system (Figure 3). Declines in the abundance of Blacksmith Lapwing and Little Egret have been relatively small (Figure 3k, 1). By contrast, declines in the abundance of the majority of species have been substantial, either proportionally as with Wood Sandpiper, Marsh Sandpiper, Common Greenshank, Ringed Plover and Kittlitz's Plover (Figure 3a–c, g, h), or both proportionally and numerically as with Curlew Sandpiper, Little Stint, Ruff,



Note: Vertical whiskers show 95% confidence limits of means in each decadal period. Colouring of bars is used to categorise species into one of four groups depending on the pattern of change in abundance across the study period, where red = species with a low-high-low pattern, with significant increases in the decades after 1980s, a high in either the 1990s or 2000s, followed by a decline in the following decade or decades, green = species increasing significantly in one or more decades, blue = species decreasing significantly over time and particularly relative to abundances in the 1980s, and yellow = species with consistently low abundance, and/or for whom no substantial change in average abundance between decades was apparent.

FIGURE 2: (a–q) Average abundances of shorebirds on the Swartvlei system over four decades, where 1980 = period 1980–1989, 1990 = period 1990–1999, 2000 = period 2000–2009 and 2010 = period 2010–2019.

Figure 2 continues on the next page \rightarrow



Note: Vertical whiskers show 95% confidence limits of means in each decadal period. Colouring of bars is used to categorise species into one of four groups depending on the pattern of change in abundance across the study period, where red = species with a low-high-low pattern, with significant increases in the decades after 1980s, a high in either the 1990s or 2000s, followed by a decline in the following decade or decades, green = species increasing significantly in one or more decades, blue = species decreasing significantly over time and particularly relative to abundances in the 1980s, and yellow = species with consistently low abundance, and/or for whom no substantial change in average abundance between decades was apparent.

FIGURE 2 (Continues...): (a-q) Average abundances of shorebirds on the Swartvlei system over four decades, where 1980 = period 1980–1989, 1990 = period 1990–1999, 2000 = period 2000–2009 and 2010 = period 2010–2019.

Pied Avocet and Grey Heron (Figure 3d, Figure 3e, Figure 3f, Figure 3i, Figure 3j).

Neither Purple Heron (Figure 3m) nor Black-winged Stilt (Figure 3n) showed any consistent or significant pattern of change in abundance in different decades.

Increases were noted in the abundance of the intermittently occurring Greater Flamingo (Figure 3o) and now established Glossy Ibis (Figure 3p). The abundance of Greater Flamingo on the Touw system was highly variable in the 2010s, with resulting high statistical variance of the mean value. The average abundance of the relatively uncommon African Spoonbill on the Touw system, although exhibiting a slow upwards trend, as observed on the Swartvlei system, does not differ significantly between most decades (Figure 3q).

Abundance trends: 1992 onwards

Decreases in abundance in the WLC as a whole have occurred for four migratory shorebirds, namely Wood Sandpiper (Z = -4.681, p < 0.01) (Figure 4c), Marsh Sandpiper (Z = -4.473, p < 0.01) (Figure 4d), Curlew Sandpiper (Z = -3.735, p < 0.01) (Figure 4e) and Ruff (Z = -4.549, p < 0.01) (Figure 4f) throughout the WLC during summer counts. Declines in the abundance of Marsh Sandpiper were most prominent on Rondevlei (Z = -3.894, p < 0.01) and Curlew Sandpiper on Swartvlei Estuary (Z = -1.948, p < 0.05).

The abundance of Black-winged Stilt in the WLC declined during winter (Z = -3.043, p < 0.01) (Figure 4i) though significant trends were only evident on Swartvlei Estuary

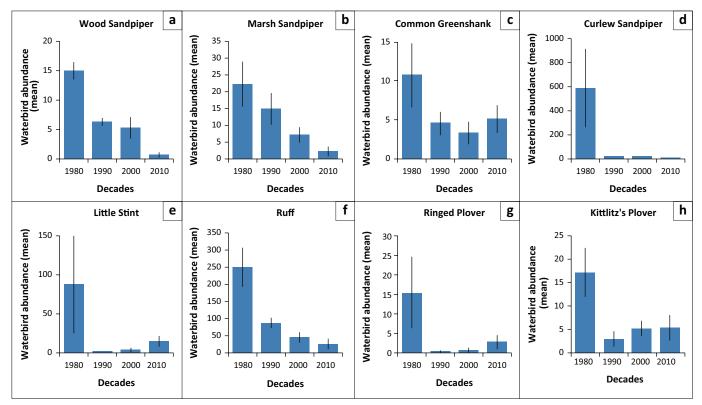
(*Z* = -3.125, *p* < 0.01). Grey Heron displayed contrasting trends of change on different waterbodies with significant increases on Touw Estuary during winter (*Z* = 1.820, *p* < 0.05) countered by declines during winter on Eilandvlei (*Z* = -3.177, *p* < 0.01), Langvlei (*Z* = -2.359, *p* < 0.01) and Swartvlei Estuary during summer (*Z* = -2.156, *p* < 0.05), with an overall decline in abundance of his species during summer surveys (*Z* = -2.132, *p* < 0.05) (Figure 4g). The abundance of Blacksmith Lapwing has declined on several waterbodies, including all the upper lakes in the Touw system during winter surveys, as well as both Eilandvlei and Swartvlei Estuaries during summer surveys (Figure 5). Despite these widespread declines, changes in the WLC as a whole were not statistically significant in either summer (*Z* = -1.023, *p* > 0.05) or winter (*Z* = -1.445, *p* > 0.05) (Figure 5).

There were increases in the abundance of several nonmigratory shorebirds within the period under review. For example, African Spoonbill increased in abundance on both Langvlei (Z = 2.276, p < 0.05) and Rondevlei (Z = 2.207, p <0.05) during summer surveys, as well as in the WLC overall (Z = 2.712, p < 0.01) (Figure 4b). Little Egret showed a significant increase in abundance on all three of the upper lakes in the Touw system during winter, and consequently in the WLC (Z = 2.766, p < 0.01) (Figure 4j). Glossy Ibis were first recorded during bird surveys in 1995 and have since become established and are now regularly recorded on both Rondevlei and Langvlei. This species was most abundant in 2004 during summer, and has been undergoing a decline in abundance since that time (Figure 4h).

No significant long-term changes in the abundance of Little Stint and Ringed Plover were evident in the WLC or any of its waterbodies from 1992 onwards (Figure 5). The abundance of Common Greenshank has declined on Touw Estuary (Figure 5), though this is unlikely to be biologically significant as no more than one individual was ever recorded on this waterbody.

Overall, the highest number of species changes were recorded on Rondevlei and Langvlei, with nine species undergoing abundances changes in one or both seasons on each waterbody. This was followed by Swartvlei Estuary with seven species, Touw Estuary with five species, Eilandvlei with four species, and with only one, intermittently occurring species undergoing change on Swartvlei Lake. The number of species undergoing declines in the WLC exceed those increasing in abundance, with six species declining on each of Rondevlei, Langvlei and seven on Swartvlei Estuary, the three waterbodies that support the highest abundances of shorebirds.

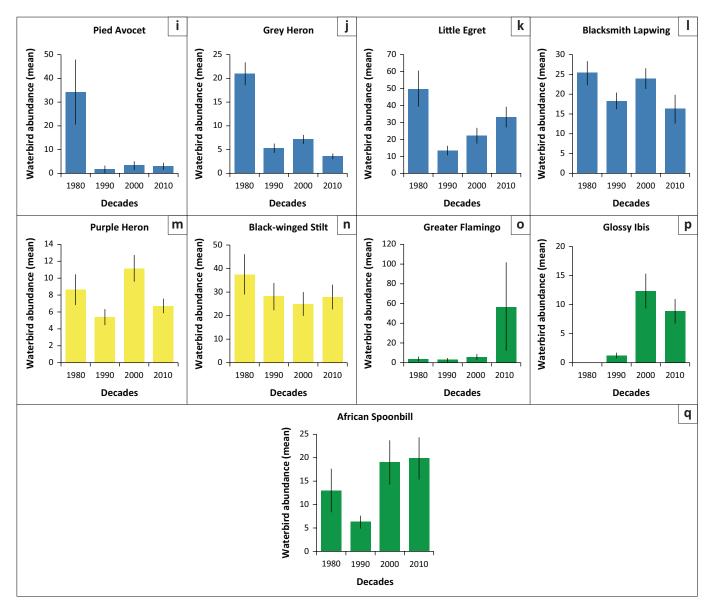
Of the species that have undergone significant changes in abundance in the WLC, the dominant pattern has been a similar direction of change across multiple waterbodies, and in different seasons, rather than the type of change differing



Note: Vertical whiskers show 95% confidence limits of means in each decadal period. Colouring of bars is used to categorise species into one of three groups depending on the pattern of change in abundance across the study period, where green = species increasing significantly in one or more decades, blue = species decreasing significantly over time and particularly relative to abundances in the 1980s, and yellow = species with consistently low abundance, and/or for whom no substantial change in average abundance between decades was apparent.

FIGURE 3: (a-q) Average abundances of shorebirds on the Touw system over four decades where 1980 = period 1980–1989, 1990 = period 1990–1999, 2000 = period 2000–2009 and 2010 = period 2010–2019.

Figure 3 continues on the next page \rightarrow



Note: Vertical whiskers show 95% confidence limits of means in each decadal period. Colouring of bars is used to categorise species into one of three groups depending on the pattern of change in abundance across the study period, where green = species increasing significantly in one or more decades, blue = species decreasing significantly over time and particularly relative to abundances in the 1980s, and yellow = species with consistently low abundance, and/ or for whom no substantial change in average abundance between decades was apparent.

FIGURE 3 (Continues...): (a–q) Average abundances of shorebirds on the Touw system over four decades where 1980 = period 1980–1989, 1990 = period 1990–1999, 2000 = period 2000–2009 and 2010 = period 2010–2019.

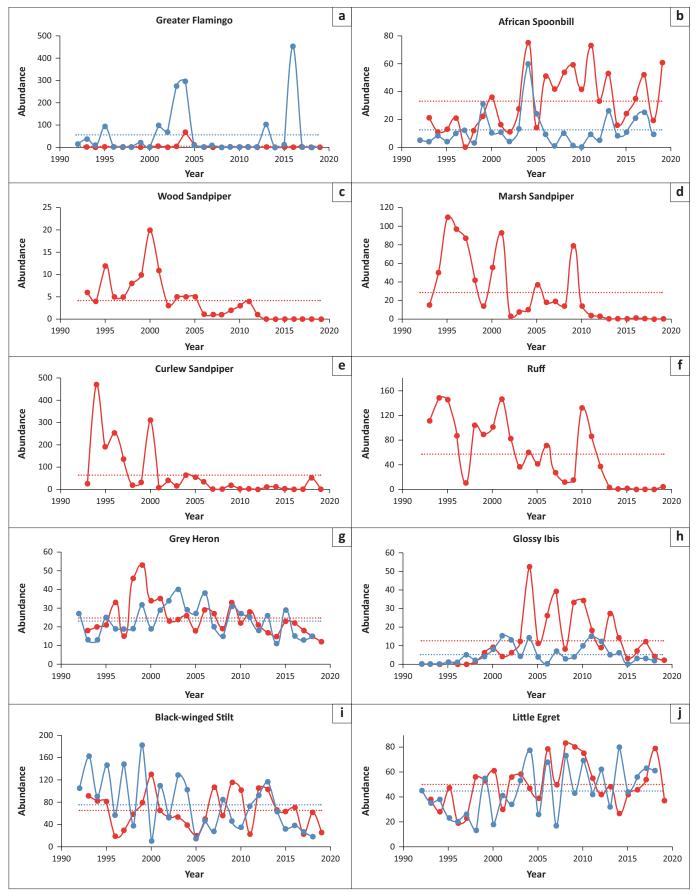
either spatially or temporarily (Figure 5) except the African Spoonbill on Rondevlei and Grey Heron on Touw Estuary during winter surveys. These species typically have low abundance on those waterbodies (averaging no more than two individuals each) (Table 1) and thus the deviations are unlikely to be biologically significant.

Discussion

Seasonal differences in shorebird abundances

The majority of shorebirds that are seasonally more abundant in the WLC in summer are Palearctic migrants (Ringed Plover, Wood Sandpiper, Marsh Sandpiper, Common Greenshank, Curlew Sandpiper, Little Stint) which migrate from the northern to the southern hemisphere during the astral summer (eds. Hockey et al. 2005). Seasonal differences in the abundance of these species in the WLC are pronounced, during winter months (Table 1). The observed seasonality of three non-migratory species differed from earlier studies. Boshoff et al. (1991) recorded higher abundances of Kittlitz's Plover and African Spoonbill in the WLC in winter, whereas in this study higher abundances of African Spoonbill occurred in summer, and Kittlitz's Plover was largely nonseasonal. Furthermore, Boshoff et al. (1991) observed the abundance of Blacksmith Lapwing to be largely non-seasonal, yet in this study higher abundances occurred during summer. Although Blacksmith Lapwing can breed opportunistically throughout the year, the majority breed between July and October (Turpie, Ryan & Tree 2005); therefore, comparatively higher summer abundances may, in part, be because of an increased abundance of fledged though not yet dispersed individuals. Glossy Ibis have become established relatively recently in the WLC, first recorded in 1995, and are typically

with only few, non-breeding individuals being present



Note: Blue solid lines and markers depict average annual abundances in winter surveys, and red solid lines and markers depict average annual abundances in summer surveys. Stippled lines show average abundances across the study period.

FIGURE 4: (a-j) Abundances of shorebirds in the Wilderness Lakes Complex showing significant changes in abundance from 1992 onwards in at least one season.

Seasonality	Species	W	LC	RV		LV		EV		TE		SVL		S	VE
		Slope		Slope		Slope		Slope		Slope		Slope		Slope	
		S	W	S	W	S	W	S	W	S	W	S	W	S	W
Winter	Greater Flamingo	\checkmark	-	-	-	-	-	-	-	-	-	-	¥	-	-
Summer	African Spoonbill	↑	-	1	¥	↑	-	-	-	-	↑	-	-	-	-
	Blacksmith Lapwing	-	-	-	\mathbf{V}	-	\mathbf{V}	\mathbf{V}	\mathbf{V}	-	-	-	-	$\mathbf{+}$	-
	Ringed Plover*	-	-	-	-	-	-	-	-	-	-	-	-	-	
	Wood Sandpiper*	\checkmark	-	1	-	\mathbf{V}	-	\mathbf{v}	-	-	-	-	-	\mathbf{V}	
	Marsh Sandpiper*	\checkmark	-	1	-	\mathbf{V}	-	-	-	-	-	-	-	\mathbf{V}	
	Common Greenshank*	-	-	-	-	-	-	-	-	\mathbf{V}	-	-	-	-	
	Curlew Sandpiper*	\checkmark	-	1	-	\mathbf{V}	-	-	-	-	-	-	-	\mathbf{V}	
	Little Stint*	-	-	-	-	-	-	-	-	-	-	-	-	-	
	Ruff*	\checkmark	-	↓	-	Ŷ	-	-	-	-	-	-	-	¥	
Non-seasonal	Grey Heron	\checkmark	-	-	-	-	¥	-	¥	-	↑	-	-	↓	
	Purple Heron	-	-	-	-	-	-	-	-	-	1	-	-	-	1
	Little Egret	-	1	-	-	1	1	-	1	\mathbf{V}	1	-	-	-	
	Glossy Ibis	1	-	1	-	1		-	-	-	-	-	-	-	
	Kittlitz's Plover	-	-	-	-	-	-	-	-	-	-	-	-	-	
	Pied Avocet	-	-	-	-	-	-	-	-	-	-	-	-	-	
	Black-winged Stilt	-	Ŧ	-	-	-	-	-	-	-	-	-	-	-	

Note: Red down arrow = significant decline in abundance within the study period; Green up arrow = significant increase in abundance within the study period; dash = no significant trend within the study period . Test statistics provided in Appendix 1.

*, Palearctic migrants.

WLC, Wilderness lakes complex comprising all the hereafter mentioned waterbodies; RV, Rondevlei; LV, Langvlei; EV, Eilandvlei; TE, Touw Estuary; SL, Swartvlei Lake; SE, Swartvlei Estuary; S, summer counts; W, winter counts. Test statistics provided in Appendix 1.

FIGURE 5: Graphic depiction of the test results of the Mann–Kendall tests performed on selected shorebird abundance data on each waterbody collected between 1992 and 2019, and combined-data for waterbodies, per season, to test for the significance and direction of non-seasonal trends.

more abundant during summer (Randall et al. 2007). This largely accords with this study where summer abundances of Glossy Ibis are more than double what typically occurs in winter, and its listing as non-seasonal (Table 1) is likely more a monitoring artefact than an accurate reflection of seasonal differences in abundance.

Seasonal differences in the abundance of shorebirds can differ between the largely natural WLC and artificial wetland habitats in the Western Cape. While the abundance of several non-migratory shorebirds, such as Grey Heron, Purple Heron, Little Egret, Glossy Ibis, Kittlitz's Plover and Blackwinged Stilt did not differ seasonally in the WLC, in artificial wetlands such as Strandfontein and Paarl (Harebottle et al. 2008) Waste Water Treatment Works most resident nonmigratory shorebirds increased in abundance in winter months (Essig 2016; Harebottle et al. 2008). The movement of birds between locations will be influenced by the suitability of habitats across their range for life history requirements including feeding, breeding and shelter, as well as factors such as weather and disturbance. Subtle differences in the relative seasonal abundances of shorebirds between natural and man-made wetlands may be driven, in part, by these factors. Natural aquatic systems found within formal conservation areas such as the WLC, with reduced disturbances, may provide more predictable and stable conditions resulting in different residence times compared to highly modified, disturbed systems such as some artificial wetlands.

Changes in shorebird abundances

Worldwide the populations of migratory shorebirds have undergone significant declines, with changes recorded in multiple species and regions including parts of Europe (Catry et al. 2001:443), Africa (eds. Delany et al. 2009) and North America (Zöckler et al. 2003:203). The families Charadriidae (including plovers and lapwings), and Scolopacidae (including sandpipers, stints, ruff and 'shanks') which comprise a high percentage of Palearctic migrants, are among the most affected, showing global declines of 51% and 54% respectively (Wetlands International 2006), which matches declining trends observed in the WLC. Declines in migratory shorebird have been particularly prominent in Africa, which is the region where the second greatest declines have occurred (Wetlands International 2006). Alternatively, Recurvirostridae (including stilts and avocets), of which southern African species do not undertake intercontinental or long distance migration (eds. Hockey et al. 2005), are typically stable or increasing globally (Wetlands International 2006; Zöckler et al. 2003) which matches the absence of system-wide declines in the WLC of the majority of non-migratory species.

Declining migratory shorebird populations are, in the southern African context, not unique to the WLC, with longterm surveys recording decreasing abundances on artificial wetlands such as Strandfontein Waste Water Treatment Works (Essig 2016) as well as large natural waterbodies such as Langebaan Lagoon (Harebottle et al. 2006), and St Lucia Estuary (Taylor et al. 1999), and coastal wetlands in the

Western Cape (Ryan 2013; Underhill 1987) and Namibia (Simmons et al. 2015). Whereas migratory wader abundances are decreasing, resident wader abundances at an artificial wetland such as Strandfontein Waste Water Treatment Works are either stable or increasing (Essig 2016). Anomalies to this trend in the WLC, such as Grey Heron and Black-winged Stilt deserve further attention, as being largely resident and nonseasonal, localised declines are potentially caused by wetland specific or localised drivers. This is emphasised by comparisons of changes in the abundances of these two species on adjacent estuarine systems. Grey Heron has limited post breeding dispersal though can move in response to changes in habitat availability (Wanless 2005) and the coastal population of Black-winged Stilt are thought to be largely locally nomadic (Underhill et al. 1999), yet both species have undergone differing changes in the WLC compared to the adjacent Knysna Estuary where abundances are stable (Coordinated Waterbird Counts unpublished data).

Possible reasons for changes in shorebird abundances

Although much has been published about the global decline of most long distance migratory shorebirds and the potential reasons for such changes, most of it has been speculative (Zöckler et al. 2003:204). A commonly stated cause for declines is habitat degradation and transformation, particularly along flyways, resulting from processes such as increased agriculture and aquaculture activities in wetlands, urbanisation, natural system modifications (e.g. impoundments) and human disturbance (Kirby, Stattersfield & Stuart 2008). Climate fluctuation is also thought to have both direct impacts on breeding success (Ganter & Boyd 2000:300; World Conservation Monitoring Centre 2000) as well as indirect impacts resulting from changes in habitat condition in both summer and winter ranges (Zöckler 2002:26). Natural processes such as complex predator cycles on the Tundra (Underhill 1987:212) also drive natural fluctuation of population numbers.

Understanding likely causes for declines, and whether primarily international or local, is important for wetland managers, for identifying potential waterbody specific management interventions to reinstate or improve habitat suitability for shorebirds. The ongoing decline of the majority of Palearctic species on Langebaan Lagoon (Harebottle et al. 2006; Simmons et al. 2015) while resident waders on the nearby Strandfontein Waste Water Treatment Works remained plentiful, led to the conclusion that international factors could potentially be a primary cause of the reductions in abundances (Harebottle & Underhill 2006:138). However, multiple factors, operating both locally and at a broader scales, can result in changing populations of shorebirds on portions of the south-western coastline of South Africa (Ryan 2013:8). Although site fidelity of some migratory species, such as Curlew Sandpiper is considered to be high (eds. Delany et al. 2009), the dispersion of populations from more pronounced feeding sites in South Africa to more remote sites (Underhill 1987; Zöckler et al. 2003) presumably to

exploit new feeding opportunities may, in part, explain local fluctuating numbers. Both estuaries in the WLC are temporarily open/closed systems with inconsistent open and closed periods, accessibility of mudflats, and reliability of feeding opportunities for migratory shorebirds thus possibly reducing consistent annual use of these systems. Changes in the preferred wintering area of Curlew Sandpiper are suggested by increasing abundances of the southern African population overwintering on coastal wetlands in Namibia (Wearne & Underhill 2005) contrary to declines occurring on major wetland further south.

Local physico-chemical and biological environmental condition particularly in the littoral zone of wetlands, such as water depth, prey availability, vegetation cover, can influence both resident and migratory wader distribution and abundance, as illustrated both locally (Boshoff et al. 1991) and elsewhere in the world (Laubhan & Gammonley 2000; Lunardi et al. 2012). The interplay of both international and local influences (Sanderson et al. 2006:99; Thomas, Hockey & Cummings 2015:176) complicates identification of causes of declines in shorebirds, and particularly migratory species. It remains a challenge to address the causes of declines in wader population numbers.

Within the WLC, several environmental changes resulting from management actions and area usage have been documented that could potentially affect habitat suitability for shorebirds. Multiple factors, including water level stabilisation and reduction in disturbances from herbivore trampling and fire, have resulted in the colonisation of many previously exposed sandbanks with emergent tall macrophytes, particularly common reed Phragmites australis (Russell 2003). Most waders feed on largely unvegetated tidal flats and littoral edges of aquatic systems (Sanders 1999; Taft, Sanzenbacher & Haig 2008), with increasing vegetation potentially hampering resource exploitation and affecting habitat selection and availability (Laubhan & Gammonley 2000:815). Increases in bulrush Typha capensis, a common emergent macrophyte in multiple wetlands in the Western Cape, South Africa, have shown to have a negative association with wader abundances (Essig 2016; Russell, Randall & Hanekom 2014). The opposite also occurs in the WLC with localised natural die-backs of clubrush Schoenoplectus scirpoideus in shallow areas resulting in higher abundances of waders on newly exposed mudflats (Russell et al. 2014). Loss of foraging habitat on the littoral edges through continuing colonisation by emergent macrophytes could potentially be contributing to declines in the abundances of small bodied waders in the WLC.

Resource access rather than abundance can be a limiting factor for waders (Finn, Catterall & Driscoll 2008:388) with increasing water depth detrimentally affecting species abundance and composition in wader communities (Colwell & Taft 2000:51; Sanders 1999:161). Water level stabilisation occurs in the WLC with artificial breaching of the temporarily open/closed estuaries at lower than natural levels resulting in reduced post-breach drawdown, and altered timing and duration of open phases (SANParks unpublished data). 'Hydrological variability is essential for waterbird communities' (Kingsford, Jenkins & Porter 2004:2490) and water level stabilisation can result in reduced waterbird diversity and abundance. Changes to the natural hydrodynamics of the WLC resulting from water level management have the potential to reduce food accessibility for particularly smaller benthic feeding waders during extended estuary closed periods.

Boating, including power boating and sailing, is permitted on several waterbodies in the WLC along with other recreational activities such as swimming, walking and fishing. Dog walking is also a popular activity along portions of the shoreline of Swartvlei Estuary where the majority of waders continue to occur. Only two waterbodies, Rondevlei and Langvlei, are closed for all recreational activities with the exception of bird watching from two fixed locality bird hides. There is an extensive published literature on the negative effects of human disturbance on birds, as reviewed by Buckley (2004) and Steven, Pickering and Castley (2011), with behavioural effects including altered site choice (Cardoni, Favero & Isacch 2008:803), and physiological changes such as increased stress levels (Müllner, Linsenmair & Wikelski 2004) and reduction in body condition and survival (Anderson & Keith 1980; Burger 1994; Velando & Munilla 2011). Even seemingly quiet and unobtrusive activities such as bird watching and photography can have significant detrimental effects (Boyle & Samson 1985:114; Şekercioğlu 2002:285). Similarly, small non-motorised boats may typically be considered to be less disturbing than motorised boats, yet their use in shallow areas not navigable by larger boats, and ability to approach slower and closer to waterbird, can result in them causing greater disturbance than larger motorised boats (Glover, Guay & Weston 2015:776). Birds tend to prefer undisturbed habitats over disturbed ones (Hockin et al. 1992), and human disturbance has been implicated in declining shorebird abundances (Ryan 2013:8), with regular disturbances able to cause sensitive birds to avoid affected areas (Végvári et al. 2011:816). High and perceived increasing recreational usage of several waterbodies in the WLC (per sobs.), and particularly during warmer summer months when migratory shorebirds occur in the region, have in all probability contributed to long-term declines in local abundance of several species.

Increases in the abundance of Little Egret on several waterbodies in the WLC is noteworthy, particularly as this is one of the colonially nesting birds that is frequently locally persecuted. Large trees in residential areas close to the WLC that support communally nesting and roosting waterbirds, which typically include herons, egrets and cormorants, are being regularly felled to force the birds to move elsewhere to minimise human disturbance and displeasure. The proliferation of Little Egret elsewhere in the world has typically been ascribed to increased feeding opportunities brought about by new flooded agricultural areas (Fasola

et al. 2010:69) and associated increases in the abundance of fish including the alien mosquitofish (Redolfi de Zan, Battistim & Carpaneto 2011:105). Reasons for increases in the abundance of Little Egret in the WLC remain unclear as adjacent wetland creation has not occurred to any significant extent, and variability of water heights within the lakes and estuaries is unlikely to have fundamentally changed as estuary breaching practices have remained unaltered throughout the waterbird survey periods. Alien fish have proliferated within the WLC (Olds et al. 2011), including mosquitofish *Gambusia affinis*, which is abundant in vegetated, shallow areas (Sloterdijk et al. 2015) and could potentially provide improved feeding opportunities for wading piscivores, including Little Egret.

Conclusions

Changes in the abundances of several shorebirds in the WLC since the 1980s have been substantial, with small migratory waders undergoing the most substantial and widespread declines. For example, in the timeframe of this study Curlew Sandpiper has gone from being the most abundant wader on Swartvlei Estuary during summer (1887 individuals in 1981) to the least abundant (zero individuals in 2019). Declines in several Palearctic migrants in multiple waterbodies within WLC, coupled with extensively reported global declines is suggestive of prominent driving factors outside of the WLC for these globally distributed species. Overall, there are multiple likely local, regional and international factors acting cumulatively rather than in isolation that are affecting shorebird changes in the WLC. Local restorative actions that could be implemented to potentially reduce anthropogenic impacts on shorebirds in the WLC could include:

- Halting the encroachment of emergent macrophytes into the lakes and reinstatement of open sand banks away from high intensity recreational areas, which can be used by shorebirds for feeding and resting.
- Reducing both the extent and intensity of disturbance from recreational pursuits and resource use activities. Declining shorebirds are typically more abundant on the estuaries, and particularly the upper reaches of Swartvlei Estuary, than other waterbodies in the WLC. Swartvlei Estuary is zoned for recreational utilisation including walking and exploring on foot, boating, swimming, bait collection and fishing. The walking of unleashed and unsupervised dogs on shorelines in the upper reaches can result in significant disturbance when dogs go swimming and chase resting or feeding shorebirds. Use zonation within park and estuary management plans could be used to restrict high disturbance activities to areas and times of low importance to waterbirds. The area of low or no usage or impact within the WLC as a whole, and particularly Swartvlei Estuary, should be increased. It is notable that the most intensive recreational use of the WLC, and particularly the estuaries, occurs during traditional school holidays in summer (December-January), which coincides with the time when migratory shorebirds occur in high number. Management of

recreational activities to reduce disturbance should be most actively undertaken in this period.

- Maintaining diversity in water heights within the WLC through resistance to the ongoing social pressure to reduce the height at which estuaries are breached will improve feeding opportunities for shorebirds, and particularly those that feed predominantly on benthic invertebrates.
- Continuing engagements for the development, improvement and implementation of national and international policies for the conservation of migratory waterbirds and protection of wetland habitats throughout their ranges.

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Appendix 1 starts on the next page \rightarrow

Appendix 1

TABLE 1-A1: Test results of the Mann–Kendall tests performed on selected shorebird abundance data on each waterbody collected between 1992 and 2019, and combined data for waterbodies, per season, to test for the significance and direction of non-seasonal trends.

Species	Season	Rond	evlei	Langvlei		Eilan	dvlei	Touw E	stuary	Swartv	lei Lake	Swartvlei Estuar		All wate	erbodies
		Ζ	р	Ζ	р	Ζ	р	Ζ	р	Ζ	р	Ζ	р	Ζ	р
Grey Heron	Summer	0.704	0.241	0.202	0.420	-1.141	0.127	-0.438	0.331	-0.487	0.313	-2.156	0.016	-2.132	0.017
Grey Heron	Winter	-0.082	0.467	-2.359	0.009	-3.177	0.001	1.820	0.034	0.020	0.492	0.279	0.390	-0.873	0.191
Purple Heron	Summer	1.601	0.055	1.612	0.053	-1.523	0.064	-0.438	0.330	0.858	0.195	1.351	0.088	0.711	0.238
Purple Heron	Winter	-0.061	0.476	0.221	0.413	-0.794	0.214	2.124	0.017	-1.198	0.115	2.111	0.017	0.516	0.303
Little Eqret	Summer	0.476	0.317	2.277	0.011	-0.267	0.395	-1.727	0.042	0.000	0.500	-0.209	0.417	1.064	0.144
Little Eqret	Winter	0.715	0.237	2.191	0.014	1.855	0.032	2.058	0.020	0.142	0.444	0.792	0.214	2.766	0.003
Glossy Ibis	Summer	2.684	0.004	2.335	0.010	0.222	0.412	-	-	0.346	0.364	-0.679	0.248	2.195	0.014
Glossy Ibis	Winter	1.221	0.111	0.000	0.500	0.637	0.262	-	-	-0.802	0.211	1.340	0.090	0.995	0.160
African Spoonbill	Summer	2.207	0.014	2.276	0.011	-0.495	0.310	0.495	0.310	1.367	0.086	-1.243	0.107	2.712	0.003
African Spoonbill	Winter	-1.856	0.032	0.630	0.264	0.395	0.346	2.186	0.014	-0.397	0.346	1.092	0.137	1.308	0.095
Greater Flamingo	Summer	-1.223	0.111	-	-	-	-	-	-	-	-	-1.000	0.159	-1.701	0.044
Greater Flamingo	Winter	0.523	0.301	0.357	0.360	-	-	-	-	-1.827	0.034	0.033	0.513	-0.867	0.193
Ringed Plover	Summer	-0.138	0.445	-0.776	0.219	-	-	-	-	-	-	0.000	0.500	0.214	0.585
Ringed Plover	Winter	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Kittlitz's Plover	Summer	0.394	0.347	0.220	0.413	-	-	-	-	-	-	-1.016	0.155	-0.128	0.449
Kittlitz's Plover	Winter	-0.698	0.243	-0.575	0.283	-	-	-	-	-0.124	0.451	-0.372	0.355	-1.034	0.150
Blacksmith Lapwing	Summer	-0.895	0.185	-0.535	0.296	-3.231	0.001	-1.135	0.128	0.042	0.483	-2.257	0.012	-1.023	0.153
Blacksmith Lapwing	Winter	-1.759	0.039	-1.890	0.029	-2.480	0.007	1.211	0.113	-1.561	0.059	-1.207	0.114	-1.445	0.074
Wood Sandpiper	Summer	-2.698	0.003	-3.169	0.001	-4.104	0.000	-	-	-0.555	0.289	-2.150	0.016	-4.681	0.000
Wood Sandpiper	Winter	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Marsh Sandpiper	Summer	-3.894	0.000	-2.579	0.005	-	-	-	-	-1.308	0.095	-3.224	0.001	-4.473	0.000
Marsh Sandpiper	Winter	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Common Greenshank	Summer	-1.552	0.060	0.950	0.171	-	-	-2.159	0.015	0.980	0.164	-1.293	0.098	-0.292	0.385
Common Greenshank	Winter	-	-	-	-	-	-	-	-	-	-	-0.777	0.218	-	-
Curlew Sandpiper	Summer	-3.101	0.001	-1.795	0.036	-	-	-	-	-1.348	0.089	-1.948	0.026	-3.735	0.000
Curlew Sandpiper	Winter	-	-	-	-	-	-	-0.990	0.161	-	-	-	-	-	-
Little Stint	Summer	-0.229	0.410	0.242	0.404	-	-	-	-	-1.348	0.089	0.767	0.222	0.652	0.257
Little Stint	Winter	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ruff	Summer	-3.648	0.000	-3.154	0.001	-	-	-	-	-1.596	0.055	-2.017	0.022	-4.549	0.000
Ruff	Winter	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pied Avocet	Summer	0.357	0.360	-0.476	0.317	-	-	-	-	0.740	0.230	0.136	0.446	0.207	0.418
Pied Avocet	Winter	-0.249	0.402	1.000	0.159	-	-	0.867	0.193	0.148	0.441	2.143	0.016	0.748	0.227
Black-winged Stilt	Summer	-1.111	0.133	1.207	0.114	-0.535	0.296	-	-	0.184	0.427	-0.919	0.179	-0.584	0.280
Black-winged Stilt	Winter	-0.623	0.267	-0.517	0.303	1.248	0.106	-	-	1.167	0.122	-3.125	0.001	-3.043	0.001